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Early testing as a means of evaluating F1 heterosis between inbred lines of Drosophila melanogaster

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EARLY TESTING AS A MEANS OF EVALUATING F_1 HETEROSIS BETWEEN INBRED LINES OF *DROSOPHILA MELANOGASTER*

by

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Signature was redacted for privacy.

Dean of Graduate College

Iowa State College
1949

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INTRODUCTION

Hybridization has been a major tool of animal and plant breeders since ancient time. Productions of hybrid corn and hybrid silkworms are of most practical significance. Hybrids are superior to available varieties.

Inbreeding followed by crossing has been effective for various species of plants and animals. Inbreeding isolates desirable characters into lines. These characters are transmitted to the progeny in predictable frequencies. The difficulty is that the inbreeding also fixes detrimental characters. Utilization of hybrids requires the formation and selection of inbreds which, on crossing, complement each other to give hybrids desirable for most characters. Good combining ability in corn is usually estimated by test-crosses or top-crosses. As carried out in corn, these tests compare hybrids resulting from crosses of inbred lines with a synthetic strain or an open-pollinated variety. In the past these tests have been made with inbred lines on the assumption that lines will remain relatively stable for combining ability through later generations of inbreeding. This procedure, if true, will hasten the evaluation and detection of superior inbred lines. The question is, will the method usually work?

The question is of even greater importance to animal breeders, as greater difficulty is encountered in isolating inbred lines of animals. Brother x sister matings, instead of selfing, must be used in our breeding system. In this system, approach toward homozygosis is less rapid than it is in selfing. Other factors, as the length of time between generations, individuals in progeny, and weak tolerance of intensive inbreeding, further complicate and increase the costs. This study had as its objective a comparison of the effects of early testing with those observed for tests of later generations, as means of isolating inbred strains of high combining ability.

Drosophila melanogaster inbreds and hybrids were established. Performance was measured by egg production. Test-crosses, both with synthetic stock and with single crosses between inbreds, were used in the evaluations of the inbred lines. Any inbred lines lost were lost through failure to reproduce and not through any conscious selection. Some partial answers to the following questions might be expected to accrue from these studies.

1. Is early testing an efficient method of predicating the general combining ability of inbred lines of later generations?

2. Does the performance of an inbred predict the performance of the hybrids in which it enters?

3. Is egg yield less for crosses made between inbred lines early in the inbreeding than when these crosses are made later in the inbreeding program?

4. What is the relative importance of general combining ability and specific combining ability as the inbreeding of the inbred lines advances?

Source of Stocks

The strains of Drosophila melanogaster used in this study had the following origins:

Amherst - This stock was collected by Dr. Philip T. Ives of Amherst, Massachusetts, from a local orchard and sent to us for this experiment.

Ames, 1943 - was collected in the wild at Ames, Iowa, in the fall of 1943. It was kept in the laboratory from 1943 to 1948, when the experiment described herein was commenced. During this period it was reproducing in large mass cultures.

Ames, 1947 - was collected from the wild at Ames, Iowa, in 1947 for use in these experiments.

Synthetic test stock - combined the characters of eight good inbred lines. The inbreds came as wild stock from widely separated places: New Jersey, Florida, Oregon, 3 Iowa, Massachusetts, and Sweden. For the Ames, Iowa, stocks the original collections were five years apart. The inbreds were crossed to form single crosses; the F_1 were bred to

form double crosses, and the double crosses bred to form the synthetic. The progeny were then crossed inter se for many generations to allow recombination and crossing over to randomize the genes.

The System of Breeding

Test for hybrid breeding performance

Fifty pairs of newly hatched flies were taken at random from each of the three strains used in this study. They were cultured in freshly prepared bottles, one bottle for one single pair. In the next generation two pairs from each bottle were selected at random and transferred into two new culture bottles. These pairs formed two sub-lines from each original line. These lines were then inbred, single pair brother x sister, for each successive generation. For the first six generations the maintenance of each line or sub-line depended on the productivity of a single pair. In this period lines were lost by lack of progeny and a few by accident. From the seventh to the twenty-fourth generation duplicate matings were prepared for each surviving line; where two successful matings occurred, only one was used to carry on the line. After 24 generations of inbreeding, quadruple matings were made to insure the continuation of each line. Where test-crosses or single crosses were produced, the flies

used were taken from the same bottle. Flies for hybrids or inbreds were random samples of the same inbred parents' progenies. The synthetic tester stock was maintained by random matings. The newly hatched flies were mixed from five stock bottles; about ten pairs from this mixture were transferred to each new food bottle. Five bottles were carried for each generation. When test-crosses were planned for the next generation, ten bottles were made to meet the demand for test-cross parents. Crosses to test the combining ability of the inbreds were made in the 1st, 8th, 9th, 16th, 23rd, and 30th generations of the brother x sister lines.

In the first generation of inbreeding a single fly in each line of each strain was test-crossed to the synthetic flies. Reciprocal crosses were made. From each bottle of hybrid progeny, six random females were bred and their egg productions on the 5th, 6th, and 7th days of their lives determined. Gowen and Johnson (1946) showed that maximum egg production ordinarily occurs on the 5th-8th days of the fly's life. The short record was a good index of the fly's total lifetime egg yield. Due to the large number of laying flies to be tested over one short period, but two hybrid virgin females from each cross were tested at one time. The first group was completed, the second commenced the next day, the third one commenced the seventh day after the first started. This technique was chosen to reduce the variations in egg productions due to date and age of bottle at test.

Each surviving line of the eighth generation was again tested by mating to the common tester, synthetic, and counting the eggs laid by the hybrid females on the 5th to 8th days. There were 59 lines involving 54 original lines and 5 sublines that survived the eight generations of inbreeding and were available for the test.

Similar matings and estimates of egg production were made on the ninth generation inbreds. Further tests with synthetic testers were made on 16th, 23rd, and 30th generation inbreds of each surviving line. Six hybrid females were used to estimate the productivity of each cross. From these tests all matings of hybrid females were made on the same day.

Tests of inbred performance

The second set of data came from pure line flies after 21, 26, and 31 generations of inbreeding. Six females were tested for egg production from each inbred line. All inbred lines were recorded on the same day when possible. The egg counts for the 31st generation inbreds and for hybrid females, inbred x synthetic, were conducted together.

Tests of single cross combinations

In the fifteenth generation four inbred lines were chosen from each inbred strain and crossed in all possible combinations. The lines used were based on the performances of their ninth generation test hybrids. The highest, the two inter-

mediate, and the lowest producing lines were chosen from each strain. To assure all cross combinations three pairs, brother x sister, were mated together in each food bottle. Two hybrid females from each cross were taken at random and their egg productions recorded.

The second test for hybrid combining ability was conducted in similar manner, but on a little larger scale. Fifteen lines of the twenty-fourth generation were chosen. Four females were used to estimate the egg production of the cross. Unfortunately, some lines used in the first test had died out. Of the twelve used in the first test nine lines were repeated in the second test.

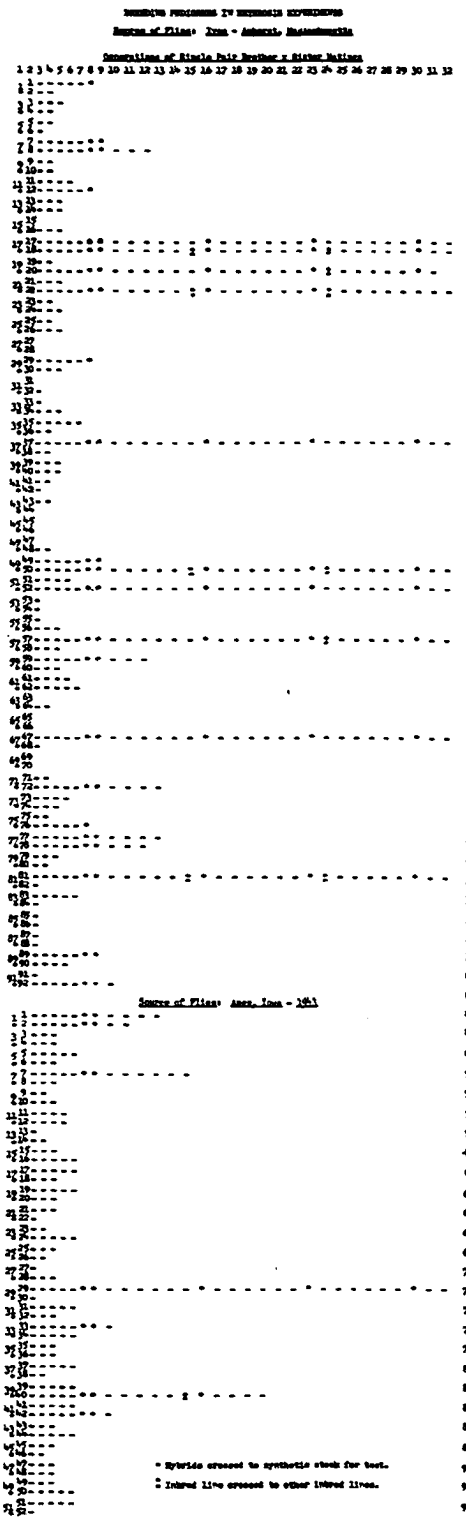
The third test for hybrid combining ability was made on twelve lines of the thirty-fourth generation of brother x sister progenies. Seven lines are represented in both the first and second tests. Four others appear in the second test.

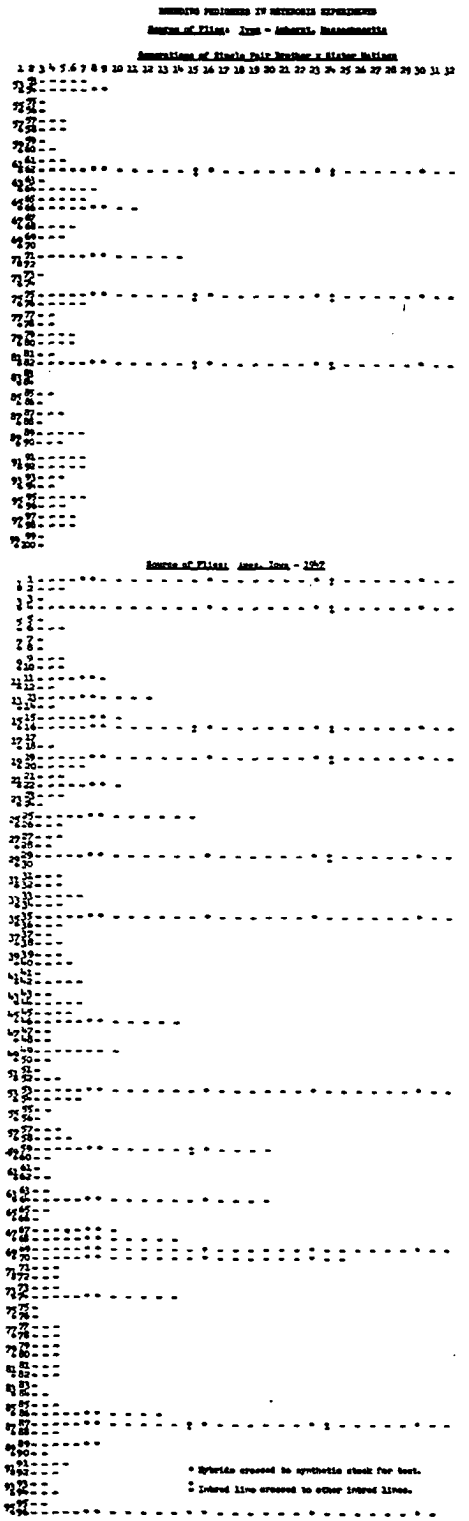
The pedigrees for each inbred line within each strain are appended, page 8.

Full egg-laying by the test females was encouraged, in the manner described by Gowen and Johnson (1946, p. 151).

> The pairs of flies tested were put in separate one fourth pint milk bottles covered with a paper cap. An egg-laying medium, composed of 10 grams of agar, 100 grams of bananas (25 grams of raisins were used instead of bananas in this study) in 400 cc. of water with enough bone charcoal added to darken the mixture, was made. With a wide mouth pipette about 1 cc. of this medium was put on the waxed surface of a milk bottle cap. When this button had hardened, a trace of 1% acetic acid was put on the surface of each with

Pedigrees on Different Lines





the moistened finger tip, and finally a small drop of a heavy yeast suspension was smeared over the surface. The caps were then ready for use.

Caps were made fresh on the first day of mating. They were renewed on the third day. And they were changed on the fifth, sixth, and seventh days at intervals of every 24 hours. The eggs laid on the caps of the fifth, sixth, and seventh days were counted.

One female was mated by two males to reduce the loss of records due to sterile males and to stimulate full-laying capacity. The males are necessary for stimulating the egg productions of their consorts. Their inheritance for productivity does not influence the productivity of females, Castle et al. (1906) and Hanson and Ferris (1929). For convenience, the males were brothers of the hybrid females taken for laying tests.

Bottles containing laying females were kept closely grouped in a cupboard. The room temperature was controlled at 26° C. Very occasionally it declined below this point due to trouble with the radiator. In summer, an air conditioner was operated to adjust the temperature close to the 26° C. point. Occasionally the temperature did reach 28 or 29° C.

REVIEW OF PERTINENT LITERATURE

The term "heterosis" was first proposed by Shull (1914) to cover the greater vigor or capacity for growth frequently displayed by crossbred animals or plants as compared with those resulting from inbreeding. He suggested that the physiological vigor of an organism is positively correlated with the degree of dissimilarity in the gametes by whose union the organism was formed. These differences between the uniting gametes need not be Mendelian in their inheritance, though the genotypic differences which stimulate activities of an organism are Mendelian in inheritance.

In 1948 Shull emphasized and redefined the word "heterosis" as having a slightly more extensive coverage than "hybrid vigor." He said, "While all hybrid vigor is heterosis, not all heterosis can be with equal propriety termed 'hybrid vigor'." The former includes the entire process that affects differences in uniting gametes from start to finish, whereas the latter is expressed only when the increased vigor is translated into visible observable phenomena.

There are several suggestions to explain the actual basic causes of heterosis. The hypotheses are not mutually exclusive. One assumes a physiological stimulation arising from the union of gametes of unlike origin. This was suggested by Shull (1908) (1910) (1911) (1914) and East

and Hayes (1912). They thought the stimulus to development came through cytoplasmic influences, greater effects being observed when certain characters are in a heterozygous condition than when they are in a homozygous condition. Vigor was supposed to increase more or less proportionately to changes in heterozygosity.

The second hypothesis attributes heterosis to the action of dominant favorable genes contributed by the two parents. A positive correlation between dominance and beneficial effect is postulated. The dominants are assumed to cover up defects which may exist in parents. The dominance theory traces to Bruce (1910), who offered a Mendelian explanation of hybrid vigor on purely mathematical grounds. Keeble and Pellow (1910) suggested dominance as an explanation for the inheritance of stature in peas. Their hypothesis of dominance led to two objections: (1) the expected skew distribution in F_2 was not found, (2) it was not possible to recover a homozygous line with multiple dominants as vigorous as the F_1 hybrids. Jones (1917) proposed the dominance of favorable linked genes as an explanation of heterosis. This suggestion removed the two earlier objections. Collins (1921) showed that even in the absence of linkage if the number of favorable dominant genes was of the order of 20 or more, the skewness and recovery of completely homozygous dominant type would be nearly impossible. This hypothesis has become the most generally used interpretation of heterosis.

Rasmusson (1933) suggested that quantitative characters are determined by series of polymeric genes. He said, "The effect of each factor on the genotype is dependent upon all other factors present, the visible effect of a certain factor being smaller, the greater the number of factors acting in the same direction." The phenomenon of dominance within the pairs of genes might be considered as only a special case of the interaction hypothesis. By use of the geometric series for the interaction hypothesis, Rasmusson derived a formula with a parameter for measuring the degree of interaction between the factors. Rasmusson showed that the inbreeding depression which may exist in practice fits well the calculated depression expected for the segregation of polymetric genes. In this view the first generation of inbreeding should show only a slight depression, whereas later generations should show a large drop. On the other hand, hybrid vigor may be inferred as depending on the combined effect of a number of cooperating factors.

East (1936) proposed a fourth hypothesis to account for heterosis. He assumed that there is a category of physiologically active as distinguished from those which are physiologically inactive genes. Physiologically active genes in a multiple allelic series may be produced by repeated mutations at a single locus. These alleles may produce a cumulative effect when unlike alleles are present. Each member of the

series of multiple alleles may have the ability to affect a different physiological process. Thus the heterozygote may be physiologically more efficient than either homozygote. Evidence for the existence of such loci is provided by the finding of Jones (1945). Apparently single gene mutations within inbred lines of corn produce heterotic effects when mutant and its allele are in heterozygous condition.

Straus and Gowen (1943) found nearly 100% increase in egg production in the cross between two inbred strains of Drosophila. By a genetic technique involving dominant markers and inversions, the 27 types representing all possible homozygous and heterozygous combinations of the first three chromosomes from two inbred lines were obtained in an experiment forming a balanced 3x3x3 factorial design. Vigor in terms of egg production was found to be linearly related to chromosome heterozygosity. Significant increases in heterosis were contributed by each chromosome pair. The total heterotic increase equaled the sum of the individual chromosome effects. Hybrid vigor was proportional to the chromosome's active length as measured by band number in the salivary chromosomes or by crossover units.

Gowen, Stadler and Johnson (1946) compared heterotic effects with cytoplasmic or chromosomal behavior. Three methods of breeding were adopted: (1) An inbred stock maintained by single pair brother x sister matings over 37 consecutive generations was continued by random mating over a

period of 10 generations, (2) the inbred stock was continued by further single pair brother x sister matings for 10 more generations, (3) the 37th generation sib inbred stock was divided into sub-lines, each of which was made "homozygous" for the first three chromosomes by genetic technique, outcrossing with inversion test stocks. The mean egg productions were 33.0, 27.4, and 21.2 eggs per fly per day for breeding systems (1), (2) and (3) respectively. The most heterozygous strain metabolized the greatest amount of energy as eggs. The most homozygous strain had the lowest production. The closely inbred strain with intermediate degree of homozygosity showed an intermediate egg yield. In (2) all the male and female gametes came from lines with a tendency toward identity of both the cytoplasmic and the genic elements. In (3) the uniting gametes were outcrosses arranged to give a majority of identical genes but diverse cytoplasms in their progeny. The lower yield in (3) ruled out the physiological stimulation hypothesis. The results showed good agreement with the hypothesis that the cause of heterosis lies in the differences in genic interaction between alleles and their reaction products.

The effect of inbreeding and outcrossing on egg production in Drosophila was first reported by Castle et al. (1906). They pointed out that, in general, inbreeding reduced productiveness slightly. Productiveness could be fully main-

tained if selection for the character was practiced along with inbreeding. In the crosses, they showed that racial fecundity of the male did not affect the production of his mate, unless he was a wholly sterile male. The crossbreds from high yield female by low male always showed high egg productions but those from low female by high male were usually, but not always, of high production. Adolph (1920) reported little change in egg yield by inbreeding. Hyde (1913) (1914) (1920) (1924) indicated there was a decline in productivity with inbreeding. Egg yields from hybrids were higher than their high producing parents. Strauss (1925) inbred Drosophila for 15-30 generations. Three lines were secured from an original pair of wild stock flies. They showed clear reduction in fertility and number of eggs laid. The restoration of the heterotic state resulted in more progeny than those obtained from any of the pure lines. Gowen and Johnson (1946) showed a decline in egg production with inbreeding even when accompanied with intense selection. A large rise in production resulted from crossing of two inbreds. Reciprocal hybrids showed variation in either direction, but were statistically alike. A like result was obtained by Straus (1942).

Similar results were found in inbred lines of guinea pigs. Wright (1922) revealed that crosses between the various strains recovered much of the vigor lost by inbreeding. Eaton (1941) made comparisons of the fertility, growth and

mortality for five inbred strains of guinea pigs, a non-inbred control stock and reciprocal crosses between the inbred strains. Vigor was greatest in the hybrids. Greater improvement over the parent strains resulted when three inbred families were combined into the hybrid than when only two were used. He indicated the performance of the hybrids could not be predicated from the performance of their inbred parents.

Gowen and Johnson (1946) published the result of an extensive study on the metabolic capacity of different races of Drosophila melanogaster for egg productions. Individual lifetime egg productions were correlated with duration of life of the female, the days the female laid, the maximum egg production in the cycle and the rate of senescence. An equation for estimating lifetime egg production was formulated.

Lifetime egg production = 19.1 3-day maximum egg production
+ 15.0 age at 3-day maximum
- 6.1 life of fly
+ 21.9 days female laid - 72.1.

The 3-day maximum egg production on the 5th, 6th and 7th days of imago life contributed 65% to the total productions. Highly significant correlations, 0.75-0.79, were obtained. From these results they suggested that any early record from the fifth to the ninth days of age would be a good index of the metabolic capacity of the fly.

Egg laying is much influenced by temperature. Delcourt

and Guyénot (1911) found that very high and very low temperatures had an inhibitory effect. The optimum temperature was 22° C. and 24° C. Straus (1942) reported egg production was highest at 25° C., lowest at 20° C., being about intermediate for the flies at 30° C.

Inasmuch as combining ability refers to the performance of inbred lines in comparable crosses, it may be considered as one of the various aspects of heterosis. Work with animals on this phase of the problem has been handicapped by lack of inbred lines.

In testing the combining ability of inbred lines of corn, the earliest method systematically crossed the inbred lines and compared the performance of the resulting crosses. Later, Jenkins and Brunson (1932) compared the performance of these lines when crossed with open-pollinated varieties. Significant correlation coefficients, from 0.53-0.90, were obtained between the two types of crosses. They concluded that "crosses with open-pollinated varieties may be used efficiently in the preliminary testing of new lines."

Johnson and Hayes (1936) found significant correlations between top-cross yields and single cross yields of 11 inbred lines of Golden Bantam sweet corn. They proved that estimates of combining ability obtained in top-crosses were approximately equal in value to estimates obtained in single crosses with several inbred lines.

Combining ability was considered an inherited character by Hayes and Johnson (1939). Most of the selfed lines obtained from the crosses between inbreds with high combining ability were higher in combining ability than were similar crosses between inbreds of low combining ability. They considered it possible to isolate inbred lines after crossing that are progressively more vigorous than those now available.

Maw (1942) studied crosses between inbred lines of domestic fowl and reported that the progeny from top-cross matings were better than those from crosses between the lines. However, Knox (1946) claimed that the results obtained from top-crosses were not any better than were obtained from out-bred progeny. In the case of poultry, the term top-cross is defined as the crossing of inbred males on outbred or relatively slightly inbred females of the same breed and variety.

Sprague and Tatum (1942) defined the term "general combining ability" as the average performance of a line in hybrid combinations and the term "specific combining ability" as those cases in which certain combinations do relatively better or worse than would be expected on the basis of average performance of the line involved. General combining ability is largely dependent on genes with additive effects and specific combining ability, on genes with dominance and epistatic effects. They concluded that "in single crosses involving previously tested lines, genes conditioning

specific combining ability have the most effect in determining yield differences." Similarly, "In previously untested material, genes affecting general combining ability are of most importance." They suggest that the top-cross tests should be used for preliminary evaluations of lines on the basis of their general combining ability, and that single-cross tests be made later to reveal the differences in specific combining abilities of the desirable lines.

Henderson (1948) estimated the general, specific, and maternal combining abilities in crosses among inbred lines of swine. Evidence for sex-linked gene effects, differences in mothering ability between lines, or general combining ability on litter characters were either non-existent or small. Specific combining ability ranged from 5 to 15 per cent of the observed variation.

Available information on the relative merits of early testing of inbred lines of corn is somewhat contradictory. Jenkins' (1935) data indicated that selection between sister progenies had been effective in choosing lines whose crosses were slightly but consistently more productive than those of their discarded sibs. He suggested that the inbred lines acquired their individuality as parents very early in the inbreeding process and remained relatively stable thereafter. The early individuality of the lines should make possible the earlier testing of them, with consequent earlier elimination of unpromising lines. He emphasized that selection for

performance should be based upon crossing tests rather than upon the appearance of the parental lines. His explanation was based on the assumption that yield is controlled by a large number of genes with equal effects. The breeding process drove equal numbers of dominants and recessives into fixation. The equal number of dominant alleles will be kept by chance through the successive generations of selfing even though accompanied by segregation for particular dominant alleles. In 1940 he published other data emphasizing the possibilities of selection for outstanding performance in hybrids between inbred lines rather than within lines. The data also add to the accumulating evidence indicating that the yield prepotency of lines in hybrids, as measured by their top-crosses, may be determined very early in the inbreeding process.

Sprague (1946) obtained results in favor of early testing. The data show that a group of lines selected for high yield and low lodging in top-crosses of the S_0 plants were high yielding and low in lodging when tested again as top-crosses in the S_1 and as single crosses in the S_3 generation. The correlation between the six S_0 lines used in his experiment and their S_1 family means was 0.85 for yield, 0.98 for stalk breaking. He concluded that the early testing procedure is of value where yield is an important consideration, where other important factors can be evaluated easily and sufficiently by the use of a suitable tester, and where the gene frequency conditioning desired characteristics other

than yield is relatively high. Two assumptions which make early testing worth while were emphasized by Sprague in the same paper. (1) Marked and stable differences in combining ability among open-pollinated plants should exist. (2) A selected sample based on tests of combining ability of S_0 (variety) or S_1 (advanced generation or a hybrid) plants should offer a greater promise of superior lines than a more nearly random sample of combining abilities drawn from the same population on the basis of visual selection alone.

Evidence opposed to these views was obtained by Singleton and Nelson (1945). They evaluated the combining abilities of successive generations of inbred sweet corn. They concluded that successive selection within inbred lines was effective in raising combining ability significantly over that of the original open-pollinated ear. They found little correlation for combining ability between the open-pollinated ear and the successive inbred generations. They recommend postponing tests for combining ability until at least the third generation of selfing.

Richey (1945) reanalyzed the data provided in Jenkins' 1935 paper. Since selection might well have been effective in some families and not in others, Richey averaged the yield for the individual families by two generation periods to smooth the data. No marked trends were found during the progress of selfing and selecting. There was lack of correspondence between early and late performance. Early testing

would have been ineffective in this material. Families altered their ranking for combining ability with successive generations of inbreeding. This was explained as being due to segregation for combining ability during the early generations of inbreeding. Richey concluded that Jenkins' data could equally well be interpreted as opposed to early testing.

Richey (1947) also examined Sprague's data. He pointed out that the opportunity for obtaining high-yielding progeny from family 130 (which yielded 10-18 bushels less than the better lines in the S_0 generation) seems to be about as good as that from the better families. He showed that only 15 per cent of the lines could have been discarded after testing in S_0 without sacrificing material prepotent for high yield.

Payne (1948) reported results of a study of combining ability when selections were made in the F_2 and F_3 generations of a single cross between two selected inbred lines, or in crossing double-cross hybrids. All the families obtained from the selfing of these single crosses were not stable in combining ability; segregation within families was occurring in F_2 and F_3 generations. He concluded that early testing for combining ability and per cent of moisture content was not an efficient method for isolating superior inbred lines.

EXPERIMENTAL RESULTS

Variation in Egg Production of First-Generation Inbreds Crossed to Synthetic Tester

To estimate early combining ability, crosses were made between the first-generation inbreds of each line and the synthetic stock. The means and the standard deviations of total egg productions on the 5th, 6th, and 7th days after hatching, for each line, are listed in Table 1. The distributions of these egg productions are shown graphically in Figure 1.

The range in egg production was similar for each strain: 20 eggs to 340 eggs. Egg production in these strains of Drosophila is highly variable. The average standard deviation is around 60 eggs, and the average coefficient of variation is about 35 per cent. This variation corresponds to that noted by Pearl (1909) for egg production in the domestic fowl: 34.2. Egg production includes a long series of activity of the female from egg formation to egg laying, related to physiological fitness. A characteristic having such a long series of antecedent characters would be expected to be influenced by many genes.

Ames, 1947, has the highest egg record, 178.8±2.5; Ames, 1943, is nearly as good, 176.2±2.7; Amherst has the lowest

Table 1. Egg productions per fly for 5th, 6th and 7th days of adult life. First generation of line x synthetic stock.

Strain Amherst - Egg Production				Strain Amherst - Egg Production			
Line No.	Mean	S. D.	C. V.	Line No.	Mean	S. D.	C. V.
1	173	40.9	23.6	45	177	73.6	41.5
3	211	46.2	21.9	47	152	61.1	40.2
5	174	59.6	34.2	49	186	45.0	24.2
7	159	67.7	42.6	51	156	66.2	42.4
9	162	55.8	34.5	53	153	65.8	42.9
11	156	62.8	40.2	55	163	59.0	36.3
13	173	77.1	44.6	57	147	43.7	29.7
15	153	63.3	41.3	59	153	63.3	41.3
17	214	51.6	24.1	61	147	56.6	38.4
19	164	46.7	28.5	63	188	71.3	37.9
21	164	50.8	30.9	65	188	58.0	30.9
23	179	58.3	32.6	67	155	68.3	44.2
25	160	59.4	37.1	69	168	62.2	36.4
29	182	86.8	47.6	71	180	75.3	41.9
31	168	59.9	35.7	75	173	58.6	33.9
33	189	57.5	30.5	77	156	59.1	37.8
35	191	62.3	32.6	83	133	54.9	41.2
37	117	42.7	36.4	88	126	62.8	49.9
39	155	99.6	64.4	90	160	57.8	36.2
41	180	49.3	27.3	91	164	98.1	59.9
43	164	67.8	41.3				
				Average (492 flies)	166.2	62.1	37.4

Table 1 (Continued)

Strain Ames, 1943 - Egg Production				Strain Ames, 1943 - Egg Production			
Line No.	Mean	S. D.	C. V.	Line No.	Mean	S. D.	C. V.
1	162	53.8	33.3	53	152	59.3	39.0
3	179	69.1	38.5	55	197	68.5	34.9
5	191	45.8	24.0	57	193	55.7	28.8
7	180	58.8	32.6	59	158	50.5	31.9
9	162	48.4	29.9	61	181	48.0	26.5
11	168	52.9	31.6	63	154	53.6	34.8
13	161	50.2	31.3	67	162	49.4	30.5
15	177	48.8	27.5	69	149	61.7	41.3
19	166	83.8	50.4	71	175	59.0	33.7
21	185	24.7	13.4	73	147	57.0	38.9
27	194	44.9	23.2	75	191	54.5	28.5
29	185	68.8	37.4	77	225	60.7	26.9
35	128	65.7	51.3	79	151	51.7	34.2
37	150	54.4	36.2	81	137	53.4	38.9
39	192	69.6	36.2	83	191	53.4	27.9
41	197	54.2	27.6	85	210	55.5	26.4
43	204	53.3	26.2	87	153	56.0	36.7
45	186	63.4	34.1	91	206	54.1	26.3
47	182	51.6	28.4	93	169	57.3	33.9
49	221	69.5	31.4	97	173	63.9	37.0
51	192	70.2	36.6				
				Average (492 flies)	176.2	59.5	33.8

Table 1 (Continued)

Strain Ames, 1947 - Egg Production				Strain Ames, 1947 - Egg Production			
Line No.	Mean	S. D.	C. V.	Line No.	Mean	S. D.	C. V.
1	161	42.2	26.1	49	181	65.9	36.4
3	201	47.1	23.5	51	179	31.7	17.7
5	175	30.5	17.4	53	188	33.5	17.8
7	156	53.0	34.1	55	173	54.4	31.5
9	195	54.9	28.1	57	188	56.8	30.2
11	156	63.0	40.3	59	204	54.5	26.7
13	218	80.5	36.9	61	198	54.2	27.4
15	218	74.8	34.3	65	190	55.3	29.0
17	179	66.2	37.1	67	173	62.9	36.3
19	175	62.5	35.8	69	178	57.7	32.5
21	197	58.4	29.6	71	189	55.2	29.2
23	179	58.7	32.8	73	162	47.7	29.4
25	184	50.2	27.2	75	192	55.2	28.8
27	182	60.1	33.1	77	174	55.8	33.9
29	198	43.7	22.2	79	167	56.2	33.7
31	174	85.3	49.1	81	169	44.4	26.2
33	191	66.4	34.7	85	175	61.4	35.1
35	200	51.9	26.0	87	197	72.5	36.8
37	164	55.6	33.9	89	142	54.4	38.3
39	170	44.0	25.9	91	150	58.8	39.1
41	179	43.9	24.6	93	130	60.7	46.9
45	169	68.0	40.2	95	192	56.4	29.4
47	174	53.3	30.7				
				Average (540 flies)	178.8	57.3	32.0

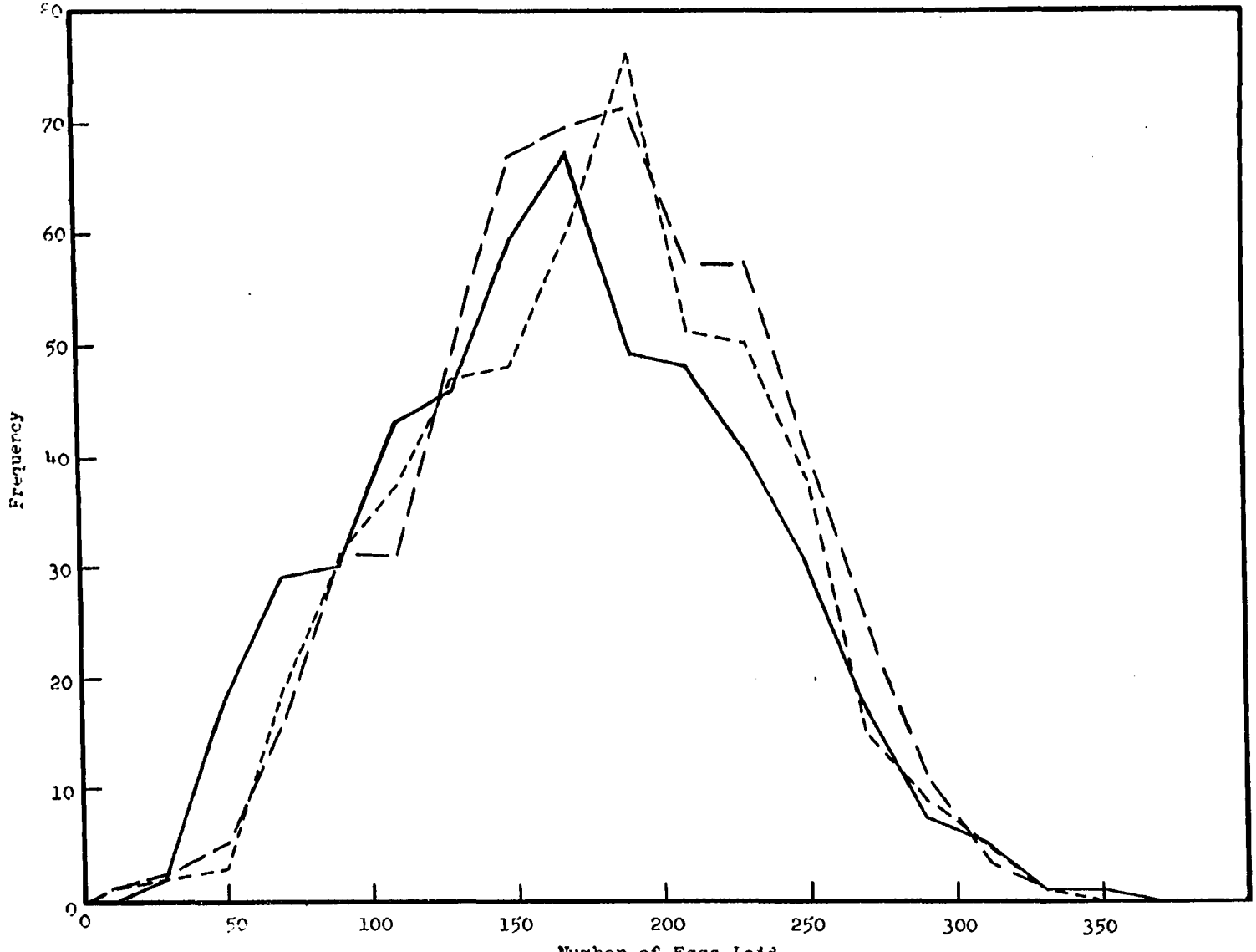


Figure 1. Distributions of egg productions for first generation, strains: ———— Amherst, - - - - - - - - Ames 1943, — — — — Ames 1947.

mean record, 166.2±2.8. The difference between the strain with the highest production and that with the lowest is 12.6 eggs. Though the average egg productions in the hybrids vary so widely, there are real differences in the combining ability between strains. These differences were investigated, using t tests.

Amherst vs. Ames, 1943 t 2.6, $P < 1\%$

Amherst vs. Ames, 1947 t 3.37, $P < 1\%$

Ames, 1943 vs. Ames, 1947 t 0.85, $P > 40\%$

The graphs in Figure 1 show frequency distributions for each group. Ames, 1943, and Ames, 1947, overlap throughout their range. Amherst shows a consistently lower productivity. Significant strain differences in combining ability exist between Amherst and Ames, 1943, and Amherst and Ames, 1947, but not between Ames, 1943, and Ames, 1947. Ames, 1943, and Ames, 1947, though collected in different years, could possibly have come from the same natural population. The similarity of these populations is an argument for the persistence of Drosophila under more extreme winter conditions than has seemed likely. In any case, the two samples, separated by five years, are not far enough apart to be differentiated into different strains in their egg production.

The distributions of egg productions of these hybrids in each strain are continuous and symmetrical. The g_1 values for Amherst, Ames, 1943 and Ames, 1947 are 0.07±0.11, -0.06±0.11 and -0.04 0.11; the g_2 -1.07±0.20, -0.41±0.20 and 0.33±0.21 respectively. These facts support the inference that a large number of genes with small additive effects are responsible for the variation.

Effects of Inbreeding on Combining Ability

The combining abilities of the different inbred strains and their sub-lines mated with our synthetic stock have been tested by counting the egg production of the F_1 females over the standard 3-day period. Inbreds of the 1st, 8th, 9th, 16th, 23rd, and 30th generation of brother x sister matings were used as one parent. Twenty-two lines from the original 300 survived to the 30th generation. These data are presented in Table 2.

The F_1 egg productions show a generally decreasing trend as the parent inbred's generation of inbreeding increases. This trend is made irregular by the 8th- and 9th-generation hybrids reacting in opposite directions. The pronounced variations indicate that uncontrolled environmental effects of some moment were influencing the flies' egg productions.

The period of egg counting for 9th-generation flies was hot. Though the room temperature was somewhat reduced by an air conditioner, the room temperature during these afternoons often reached 28-29° C. For the other tests temperatures were kept at 25.5-26.5° C. The slight rise in egg yields in the 30th generation tests may also be due to a short period with temperatures over 27.5° C. The effects of these higher temperatures may be indicated in higher egg productions. The results do not agree with those reported by Straus (1942) in

Table 2. Average number of eggs per hybrid female on 5th, 6th, and 7th da tions of brother x sister mating.

Strain Amherst	1st generation			8th generation			9th generation			16th
Line No.	Eggs	S. D.	C. V.	Eggs	S. D.	C.V.	Eggs	S. D.	C. V.	Eggs
17	214	51.6	24.1	143	25.5	17.8	200	40.3	20.2	119
18	214	51.6	24.1	146	41.6	28.5	247	51.0	20.6	87
22	164	50.8	30.9	157	31.3	19.9	203	50.1	24.7	130
37	117	42.7	36.4	160	48.5	30.3	175	57.0	32.7	105
50	186	45.0	24.2	135	29.3	21.6	197	31.7	16.1	124
52	156	66.2	42.4	155	36.3	23.4	193	49.4	25.6	140
57	147	43.7	29.7	140	48.3	34.4	195	63.8	32.7	100
67	155	68.3	44.2	121	30.3	25.1	192	71.2	37.1	100
81							186	40.3	21.7	99
Mean	169.1	52.5	32.0	144.6	36.4	25.1	198.7	50.5	25.7	111.6
Grand Mean	166.1 (592 flies)	61.6	37.5	141.7 (216 flies)	38.3	26.9	191.6 (204 flies)	50.0	24.9	111.6 (108 f
Strain Ames - 1943										
29	185	68.8	37.2	136	62.7	19.8	181.	42.2	23.4	139
62	181	48.0	26.5	148	36.2	24.5	189	67.0	35.4	126
75	191	54.5	28.5	170	56.9	33.5	238	46.5	19.6	108
82	137	53.4	38.9	122	28.1	22.9	176	46.4	26.3	111
Mean	173.5	56.2	32.8	144.0	46.0	25.2	196.0	50.5	26.2	121.0
Grand Mean	176.5 (592 flies)	56.7	32.6	136.1 (168 flies)	41.0	30.2	197.1 (132 flies)	55.0	28.0	121.1 (48 fl
Ames - 1947										
1	161	42.2	26.1	127	27.5	21.6	209	47.3	22.7	104
4	201	47.1	23.5				189	40.4	21.2	90
19	175	62.5	35.8	158	36.8	23.2	190	55.1	29.0	141
29	198	43.7	22.2	141	38.0	27.0	193	47.4	24.5	127
35	200	51.9	26.0	133	31.5	23.7	178	44.2	24.8	89
53	188	33.5	17.8	129	36.7	28.5	222	33.3	15.0	139
69	178	57.7	32.5	149	46.7	31.3	231	48.7	21.1	114
87	197	72.5	36.8	139	52.2	37.5	203	54.9	27.1	169
96	192	56.4	29.4				246	38.7	15.7	84
Mean	187.8	51.9	27.8	139.4	38.5	27.5	206.8	45.6	22.3	117.4
Grand Mean	179.7 (540 flies)	56.0	31.5	140.8 (264 flies)	41.6	29.5	197.0 (264 flies)	49.8	26.1	116.3 (144 f

Note: The average was computed from all the data available in that genera

5th, 6th, and 7th days after hatching for the lines surviving the 30 genera-

eneration		16th generation			23rd generation			30th generation		
S. D.	C. V.	Eggs	S. D.	C. V.	Eggs	S. D.	C. V.	Eggs	S. D.	C. V.
40.3	20.2	119	30.3	25.4	109	38.6	35.6	114	34.5	30.2
51.0	20.6	87	34.1	39.1	104	42.1	40.4	128	35.6	27.8
50.1	24.7	130	54.8	42.1	103	43.5	42.1	160	51.9	32.4
57.0	32.7	105	55.6	53.1	116	32.7	28.2	131	32.5	24.8
31.7	16.1	124	69.7	56.2	105	45.2	43.2	111	43.9	39.7
49.4	25.6	140	52.2	37.4	98	37.8	38.7	153	54.5	35.6
63.8	32.7	100	55.6	55.6	105	43.9	41.7	115	48.9	42.4
71.2	37.1	100	61.6	61.6	89	32.7	36.8	139	44.2	31.9
40.3	21.7	99	37.6	37.9	100	41.0	41.0	135	46.3	34.3
50.5	25.7	111.6	50.2	45.4	103.2	39.7	38.7	131.8	43.6	33.2
50.0	24.9	111.6	50.2	45.4	103.4	40.0	38.8	131.8	43.6	33.2
les)		(108 flies)			(120 flies)			(108 flies)		
42.2	23.4	139	47.5	34.2	110	41.0	29.4	102	30.0	29.6
57.0	35.4	126	48.4	38.4	127	52.7	41.6	100	38.0	38.0
46.5	19.6	108	21.2	19.6	114	56.4	49.3			
46.4	26.3	111	42.0	37.7	132	33.6	25.5	109	19.4	17.8
30.5	26.2	121.0	39.8	32.5	120.8	45.9	36.5	103.7	29.1	28.5
35.0	28.0	121.1	39.8	32.5	128.5	45.9	36.5	103.2	32.7	31.9
les)		(48 flies)			(48 flies			(48 flies)		
47.3	22.7	104	45.4	43.8	94	55.5	59.0	128	65.9	51.4
10.4	21.2	90	35.2	39.1	100	44.0	44.0	177	27.2	15.3
35.1	29.0	141	63.3	45.0	157	36.2	23.1	135	38.2	28.6
47.4	24.5	127	49.0	38.7	132	65.4	49.5	138	38.7	28.0
44.2	24.8	89	31.2	35.2	107	38.4	36.0	132	39.5	29.9
33.3	15.0	139	47.1	34.0	119	37.7	31.7	143	53.8	32.6
38.7	21.1	114	33.7	29.4	126	49.4	39.2	119	53.4	44.7
44.9	27.1	169	44.3	26.2	70	40.5	57.8	138	56.1	40.6
18.7	15.7	84	32.5	38.8				126	35.2	27.9
35.6	22.3	117.4	42.4	36.7	113.1	45.9	42.5	137.3	45.3	33.2
39.8	26.1	116.3	43.8	38.5	114.9	45.6	41.3	137.6	45.3	33.2
es)		(144 flies)			(120 flies)			(108 flies)		

able in that generation. The figures in ( ) show the number of female flies.

which egg productions were highest at 25° C., lowest at 20° C., and intermediate at 30° C.

The standard deviations and coefficients of variation for egg productions within strains are also irregular in their trends. The average standard deviation of each strain decreases but slightly as the generation of inbreeding advances. These results are unexpected. Theoretically, as the degree of inbreeding and, hence, homozygosity of the lines increases, the within-line genetic standard deviations of any character should decrease. The observed results include both genetic and environmental variances. Heterozygosity of the synthetic tester stock sampled could reduce the effects of the increasing homozygosity of the inbred lines.

The average within-line coefficients of variation show a small increase in all three strains with advancing inbreeding. This is due to the relatively big drop in the egg productions and small change in the standard deviations. Evidently, inbreeding did not endow the inbred lines of later generations with repeatable combining ability than that observed in the earlier generations.

Figure 2 graphically illustrates these results. The averages of the different strains are plotted separately. Due to the small number of degrees of freedom the regression coefficients are not significant. The irregularities of the mean yields are easily noted. The mean egg yields ranged from 104 to 206 eggs. The general trend is decreasing

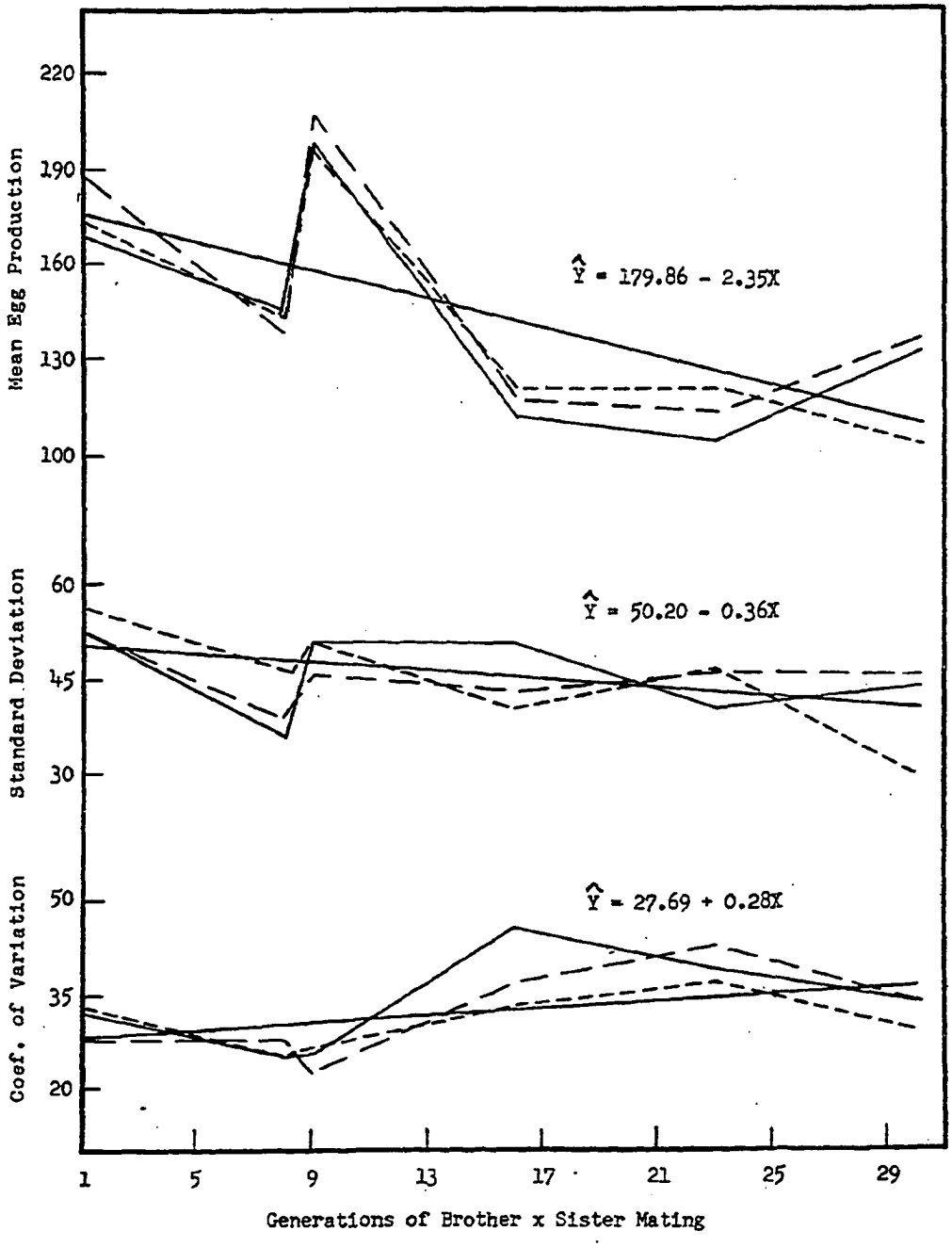


Figure 2. Means, standard deviations and coefficients of variations for top crosses from inbreds mated to synthetics plotted for each strain and generation of inbreeding: ——— Amherst ------ Ames 1943, — — — Ames 1947.

egg production with advance in inbreeding. The average decrease in the inbred x synthetic hybrids is 2.4 eggs per generation.

The within-line standard deviations range from 29 to 56. In general, they do not change much with inbreeding. They decrease 0.36 of an egg a generation. The within-line coefficient of variation increases somewhat, 0.28 per generation.

The different strains show a similar trend. This should mean that the combining abilities of the different strains should be similar. As the environmental variations were much reduced over those in nature, heredity - particularly that of the synthetic stock - should be a major cause of variation. It may be concluded that the inbred lines are still segregating in egg producing capacity expressed by test hybrids even after 30 generations of brother x sister matings.

Heterosis Exhibited by Crosses Between Inbred Lines

Fifteenth-generation inbred flies from different lines were crossed with each other to test their combining ability in the F_1 hybrids. The mean egg productions of two test females for each cross and their reciprocals (4 in all) are presented in Table 3. Similar crosses were repeated using the 24th-generation inbreds; 4 females of each cross and their reciprocals (8 in all) were tested for egg production. These data are shown in Table 4. Like crosses were made for the 34th-generation inbreds using 7 lines which were tested in the 15th and 24th generations and 4 lines which had 24th generation tests. The data are shown in Table 5.

Table 3. Heterosis of hybrid flies as evidenced by egg productions per female fly in 5th, 6th and 7th day of her life from crosses of inbred lines after 15 generations of inbreeding.

Cross	Mean F_1	Mean F_1 - P	% Increase over mean of parents	% Increase over high parent
A18xA22	169	96	132.0	83.4
A18xA81	101	24	30.8	0.2
A18xA50	107	19	20.3	-13.7
A18xB75	116	45	62.8	30.3
A18xB62	132	44	54.7	12.6
A18xB40	126	34	37.2	- 3.3
A18xB82	177	97	120.3	65.2
A18xC96	133	36	38.4	- 4.1
A18xC16	153	83	118.9	77.2
A18xC87	96	27	39.0	13.2
A18xC59	126	50	64.9	27.0
A22xA81	146	50	51.1	45.0
A22xA50	128	20	19.0	3.8
A22xB75	123	32	35.5	33.2
A22xB62	71	-34	-32.7	-40.0
A22xB40	127	16	13.7	3.1
A22xB82	107	7	7.5	0.0
A22xC96	98	-18	-15.0	-29.5
A22xC16	118	29	32.2	12.8
A22xC87	99	10	11.1	7.3
A22xC59	115	19	20.4	16.2
A22xA50	110	- 2	- 2.2	-11.3
A81xB75	82	-13	-13.2	-18.2
A81xB62	73	-36	-32.8	-37.7
A81xB40	127	11	10.2	- 2.5
A81xB82	125	21	20.1	17.1
A81xC96	84	-36	-29.9	-39.6
A81xC16	108	14	15.0	7.0
A81xC87	99	6	6.7	- 1.5
A81xC59	56	-44	-43.6	-44.0
A50xB75	143	37	34.8	16.0
A50xB62	103	-18	-14.7	-16.8
A50xB40	117	-10	- 7.7	- 5.1
A50xB82	123	8	6.7	- 0.4
A50xB96	143	12	8.8	15.6
A50xB16	133	28	26.7	7.7
A50xC87	136	57	70.1	9.7
A50xC59	94	-17	-52.8	-23.7
B75xB62	124	21	20.1	5.5
B75xB40	136	26	23.5	3.8
B75xB82	149	26	21.3	13.9

Table 3 (Continued)

Cross	Mean F_1	Mean F_1 - P	% Increase over mean of parents	% Increase over high parent
B75xC96	108	- 6	- 5.0	-22.1
B75xC16	126	38	43.0	41.0
B75xC87	116	29	33.6	30.6
B75xC59	109	15	16.2	10.4
B62xB40	89	-35	-28.4	-32.0
B62xB82	160	48	42.1	35.7
B62xC96	121	- 8	- 5.9	-26.3
B62xC16	120	18	17.9	2.3
B62xC87	132	31	29.9	11.9
B62xC59	113	5	4.4	- 3.8
B40xB82	85	-34	-28.4	-34.9
B40xC96	116	-19	-13.9	-20.1
B40xC16	126	17	16.1	- 3.4
B40xC87	119	11	10.7	- 8.6
B40xC59	104	-11	- 9.8	-20.7
B82xC96	101	-23	-18.3	-27.7
B82xC16	150	53	55.0	40.2
B82xC87	164	68	70.6	53.0
B82xC59	59	-44	-42.5	-44.6
C96xC16	175	62	55.4	26.0
C96xC87	95	-17	-15.4	-31.8
C96xC59	172	53	44.1	12.3
C16xC87	135	49	57.4	56.0
C16xC59	118	25	26.7	18.7
C87xC59	127	35	37.5	27.7
Ave. F_1	119.4±3.1			
Ave. Inbreds	101.9±6.1			
Ave. differences		17.4	20.0%	4.9 %

Note: A, B, and C are used to designate strains Amherst, Ames, 1943, and Ames, 1947, respectively.

Table 4. Heterosis of hybrid flies as evidenced by egg productions per female fly in 5th, 6th and 7th day of her life from crosses of inbred lines after 24 generations of inbreeding.

Cross	Mean F_1	Mean $F_1 - P$	% Increase over mean of parents	% Increase over high parent
A18xA20	116	17	17.0	8.0
A18xA22	118	29	33.0	29.0
A19xA50	97	-13	-11.8	-24.4
A18xA57	98	14	16.1	6.8
A18xA81	91	8	9.6	0.0
A18xB62	107	16	17.2	16.8
A18xB75	114	29	34.7	24.4
A18xB82	95	37	63.5	4.4
A18xC 1	106	5	5.2	- 3.4
A18xC 4	98	17	21.6	7.3
A18xC16	89	-29	-24.4	-38.2
A18xC19	122	36	44.2	33.3
A18xC29	92	5	5.9	0.4
A18xC87	100	-15	-12.9	-27.5
A20xA22	87	- 9	- 9.8	-19.0
A20xA50	134	16	13.7	4.7
A20xA57	107	15	16.1	- 0.6
A20xA81	95	4	4.1	-11.6
A20xB62	126	26	26.5	16.5
A20xB75	97	4	4.7	-10.0
A20xB82	103	36	54.7	- 4.5
A20xC 1	140	32	29.3	28.4
A20xC 4	104	15	16.8	- 3.8
A20xC16	132	6	5.1	- 8.1
A20xC19	104	11	12.2	- 3.6
A20xC29	119	24	25.5	10.3
A20xC87	137	15	11.8	- 0.2
A22xA50	79	-28	-26.3	-38.5
A22xA57	101	19	23.7	17.2
A22xA81	100	19	19.3	16.3
A22xB62	99	11	12.3	9.2
A22xB75	111	30	36.7	29.2
A22xB82	114	58	15.2	32.8
A22xC 1	88	- 9	- 9.3	-19.1
A22xC 4	123	45	57.9	43.2
A22xC16	105	- 9	- 8.2	-26.7
A22xC19	107	26	31.2	24.9
A22xC29	124	40	47.6	44.2
A22xC87	106	- 5	- 4.7	-22.6
A50xA57	104	2	1.7	-18.8

Table 4 (Continued)

Cross	Mean F_1	Mean $F_1 - P$	% Increase over mean of parents	% Increase over high parent
A50xA81	130	28	27.4	1.2
A50xB62	126	27	24.4	6.3
A50xB75	179	76	73.9	39.5
A50xB82	134	58	75.4	5.0
A50xC 1	181	62	52.3	41.1
A50xC 4	145	46	46.5	13.2
A50xC16	202	66	48.6	40.6
A50xC19	146	44	42.3	14.3
A50xC29	191	41	41.6	48.9
A50xC87	149	16	11.9	8.2
A57xA81	77	1	1.3	- 0.3
A57xB62	89	5	6.1	- 2.1
A57xB75	98	21	27.4	27.0
A57xB82	109	58	113.2	41.7
A57xC 1	122	29	31.1	11.6
A57xC 4	76	3	3.6	- 1.1
A57xC16	88	-23	-20.4	-33.1
A57xC19	123	46	60.0	60.7
A57xC29	131	52	65.5	60.4
A57xC87	94	-14	-12.6	-31.9
A81xB62	72	-11	-13.7	-21.1
A81xB75	101	25	32.8	31.1
A81xB82	138	87	173.9	82.9
A81xC 1	153	61	66.3	40.4
A81xC 4	159	86	119.0	21.1
A81xC16	109	- 1	- 0.8	-24.4
A81xC19	83	7	8.5	6.9
A81xC29	119	41	51.8	45.7
A81xC87	95	-24	-19.8	-30.6
A62xB75	112	28	32.9	23.0
B62xB82	103	45	76.7	12.9
B62xC 1	126	26	26.3	15.6
B62xC 4	91	11	13.2	0.2
B62xC16	224	107	91.2	55.9
B62xC19	134	50	59.7	48.1
B62xC29	116	30	34.8	28.1
B62xC87	101	-13	-11.3	-26.3
B75xB82	102	51	99.5	32.4
B75xC 1	110	19	17.7	0.5
B75xC 4	136	62	84.9	75.9
B75xC16	143	32	29.3	- 0.6
B75xC19	138	60	77.7	77.4
B75xC29	99	20	25.0	21.6

Table 4 (Continued)

Cross	Mean F_1	Mean $F_1 - P$	% Increase over mean of parents	% Increase over high parent
B75xC87	165	57	53.4	19.9
B82xC 1	109	41	61.3	- 0.7
B82xC 4	116	69	145.0	66.8
B82xC16	187	102	121.0	29.9
B82xC19	149	97	189.3	91.8
B82xC29	112	59	110.1	37.5
B82xC87	155	74	91.1	13.1
C 1xC 4	158	43	48.3	21.5
C 1xC16	127	3	2.7	- 9.7
C 1xC19	194	101	107.9	77.7
C 1xC29	163	68	70.9	49.4
C 1xC87	112	-12	- 9.3	-18.6
C 4xC16	144	39	36.2	1.0
C 4xC19	103	29	39.9	32.9
C 4xC29	146	70	92.2	78.1
C 4xC87	132	29	27.7	0.0
C16xC19	87	-23	-21.1	-39.3
C16xC29	139	27	23.6	- 3.0
C16xC87	149	8	5.9	3.5
C19xC29	74	- 6	- 6.9	- 9.3
C19xC87	104	- 4	- 3.6	-21.0
C29xC87	96	-13	-12.0	-26.4
Ave. F_1	119.5±1.7			
Ave. Inbreds	91.8±4.5			
Ave. differences		27.5	35.0	13.4

Note: A, B, and C are used to designate strains Amherst, Ames, 1943, and Ames, 1947, respectively.

Table 5. Heterosis of hybrid flies as evidenced by egg production per female in 5th, 6th and 7th day of adult life from crosses of inbred lines after 34 generations of inbreeding.

Cross	Mean F_1	Mean $F_1 - P$	% Increase over mean of parents	% Increase over high parent
A18xA22	93	- 5	- 5.1	-15.5
A18xA50	64	-33	-34.0	-41.8
A18xA81	120	23	23.7	9.1
A18xB62	94	8	9.3	-14.5
A18xB82	183	100	120.5	66.4
A18x C1	134	24	21.8	21.8
A18x C4	132	28	26.9	20.0
A18xC19	138	59	74.7	25.5
A18xC29	104	0	0.0	0.0
A18xC69	130	39	42.9	18.2
A18xC87	99	-13	-11.6	-13.9
A22xA50	124	39	45.9	42.5
A22xA81	94	8	9.3	8.0
A22xB62	109	35	47.3	25.3
A22xB82	165	93	129.2	89.7
A22x C1	102	4	4.1	- 7.3
A22x C4	95	2	2.2	- 3.2
A22xC19	169	101	148.5	94.3
A22xC29	174	81	87.1	75.8
A22xC69	164	85	107.6	88.5
A22xC87	114	13	12.9	- 0.9
A50xA81	101	17	20.2	20.2
A50xB62	104	32	44.4	25.3
A50xB82	145	75	107.1	74.7
A50x C1	85	-11	-11.5	-22.7
A50x C4	157	66	72.5	60.2
A50xC19	143	77	116.7	72.3
A50xC29	99	8	8.8	0.0
A50xC69	99	22	28.6	19.3
A50xC87	158	59	59.6	37.4
A81xB62	66	- 7	- 9.6	-21.4
A81xB82	203	132	185.9	141.7
A81x C1	203	106	109.3	84.5
A81x C4	115	24	26.4	17.3
A81xC19	140	73	109.0	66.7
A81xC29	153	62	68.1	54.5
A81xC69	96	18	23.1	14.3
A81xC87	146	46	46.0	26.9
B62xB82	94	35	59.3	51.6
B62x C1	68	-18	-20.9	-38.2
B62x C4	105	25	31.3	7.1

Table 5 (Continued)

Cross	Mean F_1	Mean F_1 - P	% Increase over mean of parents	% Increase over high parent
B62xC19	112	57	103.6	80.6
B62xC29	101	21	26.3	2.0
B62xC69	121	55	83.3	70.4
B62xC87	126	38	43.2	9.6
B82x C1	238	155	186.7	116.4
B82x C4	183	107	140.8	86.7
B82xC19	182	129	243.4	219.3
B82xC29	170	92	117.9	71.7
B82xC69	216	152	237.5	204.2
B82xC87	181	95	110.5	57.4
C1 x C4	154	50	48.1	40.0
C1 xC19	242	163	206.3	120.0
C1 xC29	235	131	126.0	113.6
C1 xC69	235	144	158.2	113.6
C1 xC87	189	77	68.8	64.3
C4 xC19	123	49	43.8	25.5
C4 xC29	139	41	41.8	40.4
C4 xC69	132	47	55.3	34.7
C4 xC87	109	2	1.9	- 5.2
C19xC29	153	79	106.8	54.5
C19xC69	197	137	228.3	177.5
C19xC87	183	101	123.2	59.1
C29xC69	146	61	71.8	47.5
C29xC87	97	-10	- 9.3	-15.7
C69xC87	99	6	6.5	-13.9
Ave. F_1	138.5±2.7			
Ave. Inbreds	85.3±5.3			
Ave. differences		53.2	68.3	39.9

Note: A, B, and C are used to designate strains Amherst, Ames, 1943 and Ames, 1947, respectively.

Sixty-six hybrid combinations were evaluated for the 15th-generation inbreds. Of this number, 47 produced more eggs than the mean of their inbred parents; 37 had higher yields than their high yielding parent. In the 24th-generation crosses, 86 out of 105 laid more eggs than the mean of their parents; 67 were higher producers than their high yielding parent. Similar results were attained in both generations. The combined data show 79 per cent of the hybrids outyielding the mean production of their parents and 61 per cent producing more eggs than their high parents. In the 34th generation, 59 out of 66 or 89 per cent laid more eggs than their inbred parental line means and 53 out of 66 or 80 per cent laid more eggs than their high parents.

The average record for the 264 F_1's from the 15th-generation crosses during the 3-day test period was 119.4±3.1 eggs. The average of 24 inbred females from the 12 lines used as parents produced 101.9±6.1 eggs. The hybrid's average increase in egg yield was 17.4 eggs or a 17.2 per cent increase over the parents. This increase is significant at nearly the 5 per cent level. When the comparison is made with the high parent, the increase is only 4.9 per cent.

The crosses involving 24th-generation lines are favorable to the hybrids. The average egg production of 840 hybrids from 105 crosses is 119.5±1.7. Sixty inbred females from the 15 lines included in the crosses have an average record

of 91.8±4.5 eggs. The hybrids produced 27.5 eggs per female more than their inbred mothers. The difference in favor of hybrids is 30.2 per cent. This difference is beyond the 1 per cent point for significance. The hybrids exceed the high parent's average egg productions by 15.4 per cent.

The crosses between the 34th generation inbred lines laid more eggs than either the 15th or 24th generation hybrids. The 528 F_1 females' mean is 138.5±2.7 eggs for the standard 3-day period. Forty-eight inbred females produced only 85.3±5.3 eggs. The difference in favor of the hybrids is 53.2 eggs or nearly 62.4 per cent. The increase over the high inbred parent is 39.9 per cent.

The average egg records of hybrid females in the 15th and 24th generations are much alike. Inbred lines in the second test averaged 10 per cent lower in yield than they did in the first test. This could result from a progressive lowering of vigor and productiveness as inbreeding increased. As 15 generations of brother x sister matings had preceded these results, it follows that reduction in vigor could continue over more generations of inbreeding than was thought heretofore. This loss of vigor is not detrimental to the hybrids which result from the union of these inbreds.

The data on the 34th generation inbreds and their F_1's bear out and accentuate these results.

The correlation coefficients between corresponding hybrid

crosses from first and second, first and third, and second and third tests are 0.25, 0.34, and 0.31 with degrees of freedom 34, 19, and 55 respectively. The first two values are non-significant. The third is beyond 5 per cent level of significance. The correlations are for limited and not strictly comparable universes. They indicate that, to a limited degree, the performance in crosses of these inbred strains can be forecasted from the results of similar crosses made with earlier generation inbreds. The peculiarities of the inbred become somewhat fixed.

These facts may support the assumption that inbreeding leads to homozygosity of concealed recessive genes with deleterious effects through rare crossing over. Crossing to other lines contributes other alleles to cover up the detrimental recessives by dominance or the joint heterozygosity at that locus.

Similar evidence is found in corn breeding. Several widely used inbreds of corn become so unproductive as to be difficult to produce in regions where hybrids between them are still among the most productive individual plants. Jones (1945) found six recessive variations in inbred lines of corn. When they were crossed with the normal lines from which they originated, they showed a fair heterotic increase in several characters.

Performance of the Inbred Lines with More than 20 Generations of Brother x Sister Mating

The inbred lines which had had 21, 26, and 31 generations of brother x sister matings in their formation were tested for their egg producing ability. The egg records for the 5th, 6th, and 7th days of life are presented in Table 6.

The average performance of the three strains is shown graphically in Figure 3. Consideration of the lines within each strain shows that each line varies widely from one generation to another. These fluctuations emphasize the environmental-genotypic interactions and the importance of chance in these results. Despite these fluctuations the three strains show similar downward general trends (Figure 3). The average egg record of all available inbred lines in the 21st generation is 130 per fly in contrast to 116 eggs in the 26th generation and 90 in the 31st generation. The strains' average egg yield is reduced 4.3 eggs per generation of inbreeding, a reduction of 3 to 4 per cent. This loss is in addition to lines lost due to their inability to reproduce themselves.

A decrease in vigor in the early generations of inbreeding is concordant with the effects observed in other species. In later generations the decline should be reduced. A decline of the magnitude observed here, after more than 20 generations of brother x sister mating, is unexpected if due to the simple sorting out of randomly segregating deleterious

Table 6. Three-day egg productions per fly for inbred lines with 21, 26, and 31 generations of brother x sister matings.

Strain Amherst Line No.	21st generation Eggs	S. D.	C. V.	26th generation Eggs	S. D.	C. V.	31st generation Eggs	S. D.	C. V.
17	119	69.8	58.8	122	28.4	23.4	106	45.4	42.8
18	87	26.6	30.6	82	24.6	30.1	94	34.1	36.1
22	146	42.2	29.0	122	16.9	13.9	117	44.3	37.9
37	131	32.8	25.0	115	16.9	14.7	71	53.7	75.6
50	164	44.6	27.2	159	24.3	15.3	89	39.8	44.6
52	141	29.0	20.5	156	67.4	43.3	96	23.6	24.7
57	182	26.7	14.7	148	15.9	10.7	100	51.7	51.7
67	96	37.4	39.2	132	14.6	11.0	99	24.1	24.3
81	83	21.7	26.1	87	35.1	40.5	113	17.2	15.2
Mean	127.7	36.7	30.1	124.8	27.1	22.5	98.3	37.1	39.2
Grand Mean	126.7 (60 flies)	34.4	28.2	126.1 (60 flies)	28.0	22.9	98.3 (54 flies)	37.1	39.2

Table 6 (Continued)

Strain	21st generation			26th generation			31st generation		
Line No.	Eggs	S. D.	C. V.	Eggs	S. D.	C. V.	Eggs	S. D.	C. V.
29	48	15.3	31.8	156	30.0	19.2	82	46.8	57.1
62	136	44.7	32.8	125	24.1	19.3	83	25.2	30.5
75	110	46.1	41.9	70	17.0	24.1			
82	119	42.2	35.5	78	35.7	45.8	32	15.9	49.7
Mean	103.3	37.1	35.5	107.3	26.7	27.1	66	29.3	45.7
Grand Mean	103.3 (24 flies)	37.1	35.5	107.3 (24 flies)	26.7	27.1	66 (18 flies)	29.3	45.7
Strain Ames - 1947									
1	237	52.9	22.3	60	27.9	46.6	67	23.9	35.6
4	131	23.5	18.0	112	25.8	23.1	86	22.9	26.7
19	120	26.6	22.2	87	31.3	35.9	99	17.7	17.9
29	134	23.2	17.3	65	29.6	45.5	44	20.2	46.2
35	168	22.1	13.2	135	22.2	16.5	115	14.6	12.7
53	170	46.2	27.2	148	45.8	31.0	131	29.5	22.5
69	114	36.2	31.9	58	32.5	55.9	65	31.9	49.2
87	168	27.4	16.3	139	8.4	6.0	114	26.8	23.5
96	117	18.7	16.1	152	28.1	18.5	79	9.1	11.6
Mean	151.0	30.8	20.5	106.2	28.0	31.0	89	21.8	27.3
Grand Mean	146.7 (66 flies)	33.4	23.2	109.2 (60 flies)	27.6	29.7	89 (54 flies)	21.8	27.3

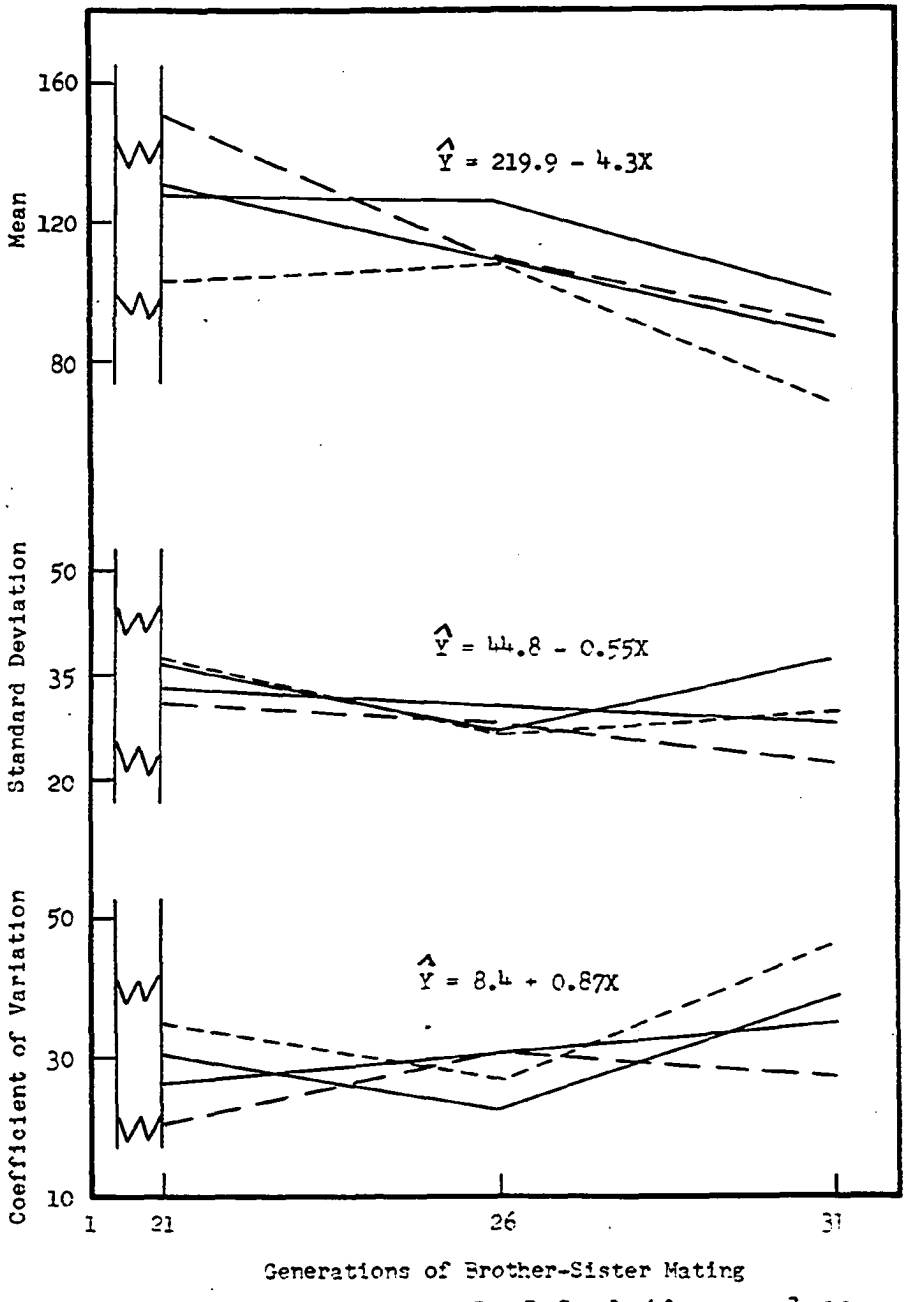


Figure 3. Means, standard deviations and coefficients of variations for inbreds plotted by generations and strains: ——— Amherst, - - - - - - - Ames 1943, — — — Ames 1947.

genes. Instead, it would appear as if either some environmental condition was at work to depress the egg productions of successive generations or some genetic mechanism was at work which kept variability within the lines in opposition to the trend toward homozygosis. The fact that the hybrids to the synthetic stock seem to have stabilized to a fairly uniform production rate after the 17th generation does not seem to favor a progressively bad environmental trend as the probable cause of the continued reduction in yield of the inbreds. Rather, it would appear as though a fairly consistent number of deleterious genes were being brought to the homozygous state and reducing production. Unfortunately the degrees of freedom are so small as to make tests of significance of doubtful value.

Analysis of Variation Within Synthetic x Inbred Crosses

Up to this point, the discussion has largely centered on the accumulated effects of inbreeding as observed on the means of strain crosses, inbred x synthetic testers, or on the means of the inbreds themselves. The experiment, as originally designed, has as possible divisions of variance, among strains, among lines within strains, among sub-lines within lines, between reciprocals within sub-lines, and individuals. Unfortunately, because so many sub-lines were lost, this arrangement had to be abandoned. The material in the following section analyzes the trends within the different lines and the reciprocal

effects due to the choice of the line as a male or female parent. These data appear in Table 7.

The uncontrolled variations for the different generations show a decreasing trend with increasing inbreeding. This change reflects better control of experimental conditions, less environmental interactions, or a reduction in chance variations. As the experimental conditions were kept nearly constant, the major cause of the linear reduction would appear to be progressive changes accompanying the inbreeding. The reduction in variation is a measure of the success of the inbreeding program and its accompanying natural selection in reducing the genotypic variation within lines and in sorting out genotypic environmental interactions which tend to reduce the variation in egg production.

The reciprocal effects are marked by irregularity. Four generations of the six are highly significant, one is significant at the 5 per cent point. The effects of the reciprocal crosses are without trend. The part played by this factor in creating variation in egg production has been essentially uniform throughout the experiment. The female genotypes from reciprocal crosses in Drosophila should be of the same constitution. Such being the case, it would seem that the only explanation of a significant difference between the reciprocal crosses would be that due to an effect of the mother's laying eggs of larger size, etc., and thus giving

Table 7. Tests for combining ability in different generations. Egg productions per fly for 5th, 6th and 7th day of adult life for lines crossed to synthetic strain.

Sources of variation	Degrees of freedom	Individuals per group	Mean square	F	Interpretation	Portion of variance: Actual units	Portion of variance: %
First generation							
Among strains	2	508	22869	4.88**	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2+508\ \sigma_s^2$	36	1.0
Among lines within strains	124	12	4566	1.05	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2$	0	0.0
Between reciprocal crosses within lines	127	6	4799	1.44**	$\sigma_e^2+6\ \sigma_r^2$	246	6.8
Individuals	1270	1	3326		σ_e^2	3326	92.2
Total	1523						
Eighth generation							
Among strains	2	213	2118	1.56	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2+213\ \sigma_s^2$	0	0.0
Among lines within strains	51	12	3311	1.01	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2$	2	1.0
Between reciprocal crosses within lines	54	6	3291	2.06**	$\sigma_e^2+6\ \sigma_r^2$	283	15.0
Individuals	540	1	1595		σ_e^2	1595	84.0
Total	647						
Ninth generation							
Among strains	2	193	1619	6.10	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2+193\ \sigma_s^2$	0	0.0
Among lines within strains	47	12	9864	1.37	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2$	221	6.4
Between reciprocal crosses within lines	50	6	7209	2.94**	$\sigma_e^2+6\ \sigma_r^2$	792	22.8
Individuals	500	1	2456		σ_e^2	2456	70.8
Total	599						

Table 7 (Continued)

Sources of variation	Degrees of freedom	Individuals per group	Mean square	F	Interpretation	Portion of variance: Actual units	Portion of variance: %
Sixteenth generation							
Among strains	2	89	5511	1.18	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2+89\ \sigma_s^2$	0	0.0
Among lines within strains	21	12	6482	2.19*	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2$	294	10.9
Between reciprocal crosses within lines	24	6	2960	1.29	$\sigma_e^2+6\ \sigma_r^2$	112	4.1
Individuals	240	1	2291		σ_e^2	2291	85.0
Total	287						
Twenty-third generation							
Among strains	2	90	11151	3.18	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2+90\ \sigma_s^2$	85	3.8
Among lines within strains	21	12	3504	1.09	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2$	25	1.1
Between reciprocal crosses within lines	24	6	3202	1.70*	$\sigma_e^2+6\ \sigma_r^2$	219	9.9
Individuals	240	1	1887		σ_e^2	1887	85.2
Total	287						
Thirtieth generation							
Among strains	2	83	20162	5.69*	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2+83\ \sigma_s^2$	180	7.6
Among lines within strains	19	12	1946	2.64*	$\sigma_e^2+6\ \sigma_r^2+12\ \sigma_l^2$	0	0.0
Between reciprocal crosses within lines	22	6	5139	3.18**	$\sigma_e^2+6\ \sigma_r^2$	587	24.6
Individuals	220	1	1618		σ_e^2	1618	67.8
Total	263						

Note: **probability is less than 1%, *less than 5%.
Error term used for reciprocal mean square is individual mean square; for among lines is that for reciprocal; for strains is that for among lines or for among lines and reciprocals whichever is larger.

the larvae of one cross a better start than those from its reciprocal. Examination of the data on the reciprocal crosses shows that the synthetic's used as females produce hybrids having the lower productions. These data are given in Table 8.

Of the 18 comparisons in Table 8, 14 show the cross inbred female x synthetic male to have the larger productions. Most of the differences are small. The average difference is 7.7 eggs. The synthetic females are the poorer mothers, possibly because the progeny per cross is greater than when the inbreds are used.

The line differences in Table 7 are likewise represented by highly irregular effects. The trend is toward less variation as the generations of inbreeding increase. In two of the six generations, the line differences are less than for those for the reciprocals. In general, line genotypes do not seem to have separated greatly from each other during the course of the inbreeding.

Strain differences in the first generation are highly significant and large. This value is in contrast to the trend displayed by the rest of the data. Generations 8, 9, 16, 23, and 30, are consistent in showing increasing differentiation in the strains with advancing inbreeding. The change is almost linear from the eighth to the thirtieth generation. The fact that this trend would lead to negative values for the early

Table 8. Mean egg productions of top cross hybrids (inbred x synthetic) for successive generations of inbreeding separated by strains and reciprocal within strains.

Generation of inbred	Total lines	inbred x tester		tester x inbred		Difference of mean	t	P
Amherst								
1	41	166.7± (22)	3.87	165.2± (19)	4.05	1.5	0.26	>0.5
8	18	155.0± (15)	3.91	129.2± (3)	3.62	25.8	4.84	<0.01**
9	17	195.9± (11)	6.11	187.4± (6)	6.11	8.5	0.98	0.3-0.4
16	9	123.1± (7)	7.18	100.2± (2)	6.83	22.9	2.22	<0.05*
23	10	110.6± (7)	5.09	96.3± (3)	4.93	14.3	2.02	<0.05*
31	9	133.6± (4)	5.55	129.9± (5)	6.79	3.7	0.42	>0.5
Ames - 1943								
1	41	170.8± (14)	3.61	181.6± (27)	3.73	-10.8	-2.08	<0.05*
8	14	143.3± (12)	3.85	128.7± (2)	4.75	14.6	2.55	<0.02*
9	11	205.5± (9)	6.52	188.8± (2)	5.49	16.7	1.96	<0.02*
16	7	124.5± (2)	10.21	117.7± (2)	10.50	6.8	0.41	>0.5
23	4	132.8± (3)	8.67	123.3± (1)	10.07	9.5	0.71	0.4-0.5
31	4	113.3± (3)	6.67	92.7± (1)	6.51	20.6	2.21	<0.02*

Table 8 (Continued)

Generation of inbred	Total lines	inbred x tester	tester x inbred	Difference of mean	t	P
Ames - 1947						
1	45	182.7±3.30 (26)	179.9±3.65 (19)	7.2	1.46	0.1-0.2
8	22	141.2±3.78 (11)	141.9±3.93 (11)	-0.7	-0.13	>0.5
9	22	204.3±4.91 (13)	189.6±6.60 (9)	14.7	1.78	0.1-0.5
16	12	111.2±5.98 (5)	121.3±5.46 (7)	-10.1	-1.25	0.2-0.3
23	10	118.2±6.89 (5)	111.7±5.89 (5)	6.5	0.71	0.4-0.5
31	9	133.9±6.48 (3)	141.4±6.45 (6)	-7.5	-0.82	>0.4
Mean		148.1	140.4			

Note: 1. Average egg production includes the total of the eggs laid by the 5th, 6th and 7th day of her life.

2. ( )The number of lines in cross with higher records than their corresponding reciprocal cross.

generations mean squares indicates a displacement of the curve in space if the trend itself is correct. The weight of the evidence suggests that the continued inbreeding has caused an increasing separation of the strains in their egg productions. This accentuation of the strain differences with inbreeding points to some reorganization of each strain toward homozygous but different types during the course of the inbreeding program.

The analysis of the variance contributions of each factor on a unit basis are shown in the right-hand column of Table 7. The percentage contributions of the uncontrolled variance range from 68 to 92. Differences between reciprocals range from 4 to 24 per cent. The line contributions are small and irregular. Strain effects are zero for the first sixteen generations. After the twenty-third generation, the strain effects become more pronounced, rising to 4 per cent in the twenty-third and 7.5 per cent in the thirty-first generation of inbreeding.

Analysis of Variation Within the Inbred Lines After Twenty Generations of Brother x Sister Mating

The variations of the 21st, 26th, and 31st generations of the different inbred lines are shown in Table 9. The uncontrolled variations within the lines are quite similar, ranging from 1026 to 1409 with a mean of 1275. The pure inbreds have 72 per cent less variation than was observed for the inbreds x synthetic over all the generations tested. For corresponding

Table 9. Variance of egg productions per fly for 5th, 6th and 7th day of adult life for pure inbred lines in 21st, 26th and 31st generations.

Sources of variation	Degrees of freedom	Individuals per group	Mean square	F	Interpretation	Portion of variance Actual units	Portion of variance %
			Twenty-first generation				
Among strains	2	47	17768	2.0	$\sigma_e^2+6\,\sigma_1^2+47\,\sigma_s^2$	186	6.5
Among lines within strains	22	6	9110	6.0**	$\sigma_e^2+6\,\sigma_1^2$	1286	44.9
Individuals	125	1	1391			1391	48.6
Total	149						
			Twenty-sixth generation				
Among strains	2	45	5446	1.3	$\sigma_e^2+6\,\sigma_1^2+45\,\sigma_s^2$	0	0.0
Among lines within strains	21	6	7025	5.0**	$\sigma_e^2+6\,\sigma_1^2$	936	39.9
Individuals	120	1	1409			1409	60.1
Total	143						
			Thirty-first generation				
Among strains	2	39	7323	1.9	$\sigma_e^2+6\,\sigma_1^2+39\,\sigma_s^2$	92	5.8
Among lines within strains	18	6	3782	3.7**	$\sigma_e^2+6\,\sigma_1^2$	459	29.1
Individuals	105	1	1026			1026	65.1
Total	125						

periods, the pure inbreds have 37 per cent less variation than the top cross testers. The differences in uncontrolled variations appear to come from the heterozygosity of the synthetic stock used as one parent in the top cross test.

The mean squares between the inbred lines range from 3782 to 9110 with an average of 6639. The differences between lins within strains are highly significant for each generation. The mean squares are 68 per cent greater than those observed for corresponding periods of the inbred x synthetic top cross tests. The behavior of the different lines accords with expectation since the inbreds should be fairly well differentiated by the 21st generation of brother x sister mating whereas the test crosses to synthetic always have the variability of the synthetic stock to create variability in the crosses.

The strains show differences in performance which are not significant as contrasted with the mean squares observed for lines within strains. These differences contribute 4 per cent to the variation. The differences fixed within lines add 38 per cent to the variance. The individual totals represent the remainder, 58 per cent. The egg yields show a fair differentiation of the lines but not exactly in the way expected since the line differentiation has decreased from the 21st to the 31st generation.

Relation Between Early and Later Generation Tests for Combining Ability, Top Crosses and Inbreds

The preceding data contribute information on the value of early testing. Correlation coefficients between the egg productions of different generation tests were computed. The results are given in Table 10. The correlations are given for each reciprocal and for the combined data.

The correlation coefficients between successive top crosses range from 0.25 to -0.37 with an average of -0.01. The correlations show no trends of any moment. For this material the top cross test on one generation seems to have no predictive value for the performance of a like cross in another generation. The separation of these data into their reciprocals increases the variation but does not change the conclusion.

The correlations between the performance of like inbred lines in different generations of inbreeding are positive. Two of the correlations are small, one is significant at the 5 per cent level. The average value is 0.25. These results are supported by the data on the inbreds of the 15th, 24th, and 34th generations which were used to form F_1 crosses. Inbred performance in one generation is a better index of future performance than like tests made on top crosses.

Table 10. Correlation coefficients between egg productions per fly on 5th, 6th, and 7th day of imago life from different generation top cross tests.

Generations in comparison	Number of lines paired	inbred x synthetic	synthetic x inbred	All top crosses
1st & 8th	62	-0.27*	0.15	0.01
1st & 9th	56	0.08	0.17	0.05
1st & 16th	24	-0.24	-0.09	-0.07
1st & 23rd	23	-0.32	0.46*	0.11
1st & 30th	21	-0.17	-0.13	0.06
8th & 9th	56	-0.19	0.13	0.08
8th & 16th	23	-0.06	-0.13	-0.12
8th & 23rd	22	0.20	-0.02	0.25
8th & 30th	19	-0.05	-0.04	0.05
9th & 16th	23	-0.16	-0.20	-0.24
9th & 23rd	24	-0.56**	0.16	0.14
9th & 30th	22	-0.22	-0.11	-0.09
16th & 23rd	23	-0.29	+0.20	-0.08
16th & 30th	22	-0.11	0.00	-0.01
23rd & 30th	21	-0.07	-0.17	-0.37
Mean		-0.16	+0.02	-0.01
	Inbred line correlations			
21st vs 26th	24			0.12
21st vs 31st	21			0.09
36th vs 31st	21			0.53*
Mean				0.25

Evaluation of General and Specific Combining Ability, Etc.

General combining ability is defined as an average record of the line when crossed to other lines. In use, this average is contrasted with similar averages of other lines tested in like periods. To be unbiased, the crosses from which these averages are obtained should be made at the same time and with equal numbers.

Specific combining ability is defined as the amount by which the average performance of a designated cross involving a line is better or worse than the average of all crosses having this line as one parent.

Several methods have been worked out to estimate these values. For the purposes of our analysis the latest method, described by Henderson (1948), appears most appropriate. The record for any particular animal of a cross is assumed to be determined by the following elements according to the equation:

$$y_{ijk} = u + g_i + g_j + m_j + s_{ij} + r_{ij} + e_{ijk}$$

u = mean of all lines.

g_i (or g_j) = general combining ability of g_i (or g_j) line when mated to the other lines combined in the particular crosses.

m_j = effect peculiar to the j^{th} line when used as the female parent.

s_{ij} = specific combining ability of the reciprocal crosses for the i^{th} line with the j^{th} line.

r_{ij}= effect common to all progeny of i males x j females not accounted for by g_i or g_j, m_j or s_{ij}. Sex linked genes could cause effects of this type.

e_{ijk}= individual variation not accounted for by the above postulated factors.

The methods of calculating these different constants and their contributions to variance are given by Henderson in the above reference (1948).

The data for the different crosses are presented in Tables 11, 12, and 13.

The variance analyses of Tables 11, 12, and 13 lead to the data shown in Table 14.

The data of Table 14 show that there are significant effects attributable to each postulated cause of variation in Drosophila egg production. General combining ability shows the greatest significance. The components of variance for different generations are shown in Table 15.

The estimates of the components of variance σ_e^2, σ_r^2, σ_s^2, σ_m^2, and σ_g^2 in Table 15 are relative and dependent upon the particular cross-combination of lines involved. The results among the three tests are not quite comparable as some of the lines crossed were not the same in different generations. The general results should be fairly representative.

Table 11. F_1 hybrid egg production of 15th generation inbred parents.

			Male lines												F_1 Total
			Amherst				Ames 1943				Ames 1947				
		Line no.	18	22	81	50	75	62	40	82	96	16	87	59	
Female lines	Amherst	18	93 14	103 115	150 147	90 97	74 94	141 162	152 187	202 170	129 223	114 166	36 121	28 189	2920
		22	265 192	74 110	161 70	117 111	162 100	57 48	143 164	81 69	57 144	68 176	69 71	83 132	2540
		81	77 29	211 141	100 101	81 116	71 85	67 60	100 180	52 66	91 95	104 104	81 101	72 52	2036
		50	122 117	181 104	161 80	126 121	181 193	127 135	115 82	162 64	189 117	114 176	172 93	73 128	2916
	Ames 1943	75	58 238	99 129	85 88	116 83	130 48	168 59	48 81	140 147	85 150	59 116	64 132	128 124	2397
		62	114 112	80 97	60 106	81 68	58 211	136 99	86 103	130 100	136 98	106 61	108 108	86 72	2181
		40	83 83	102 97	106 123	84 158	182 231	72 94	107 154	88 112	144 137	166 157	98 100	99 102	2618
		82	71 264	130 148	176 207	163 103	178 132	228 180	65 75	125 89	69 137	272 217	136 175	12 96	3234
	Ames 1947	96	62 119	91 100	48 102	135 130	128 70	143 106	90 93	128 68	92 186	187 187	80 29	184 159	2439
		16	204 99	63 165	87 135	181 61	130 197	240 74	84 97	66 45	156 171	107 66	37 88	108 196	2684
		87	161 67	113 142	95 119	176 101	149 120	150 160	195 84	172 172	154 116	171 244	77 93	128 87	3076
		59	83 203	107 138	42 59	38 138	112 73	73 221	105 108	69 60	184 159	57 109	179 112	83 115	2429
F_1 Total			2823	2656	2407	2428	2931	2765	2467	2363	2491	3161	2190	2338	31470

Table 12. F_1 hybrid egg productions of 24th generation inbred parents.

Female lines		Line no.	Male lines: Amherst 18	20	22	50	57	81	Ames 1943 62	75	82	Ames 1947 1	4	16	19	29	87	F_1 Total
Amherst		18	114	178	112	62	80	115	101	44	119	185	111	67	193	84	66	6168
			79	136	134	40	105	80	104	26	97	100	130	77	210	133	101	
			84	108	74	42	110	98	85	67	80	173	88	58	135	133	94	
			88	121	218	152	228	136	138	45	92	68	111	88	137	115	124	
		20	87	138	103	128	83	97	120	109	104	108	89	134	105	180	125	5798
			56	134	92	100	61	70	132	85	99	122	130	80	99	137	169	
			97	82	81	84	50	61	108	91	76	120	68	64	101	105	143	
			148	77	118	133	53	115	146	129	84	151	60	52	82	128	146	
		22	65	49	104	69	106	95	61	102	94	99	122	143	89	143	154	5990
			104	124	80	63	91	101	138	116	85	92	151	126	115	144	106	
			99	44	82	143	119	166	70	127	128	103	90	156	79	155	129	
			106	87	77	80	91	125	97	120	86	82	88	69	76	218	111	
		50	93	160	73	131	80	175	119	109	96	124	124	210	174	200	161	7673
			158	184	47	107	49	107	153	105	92	183	188	163	205	204	121	
			144	126	98	141	83	170	102	94	111	106	189	275	67	219	109	
			83	157	57	133	73	100	108	96	100	273	205	206	126	166	173	
		57	75	102	77	156	99	75	111	93	76	155	52	95	163	196	132	5956
			49	207	61	110	70	66	80	61	65	108	63	99	133	188	105	
			55	136	136	163	77	105	80	41	41	216	100	115	122	167	115	
			73	165	123	117	61	63	106	127	42	185	87	53	89	70	106	
		81	82	125	94	93	82	82	94	107	115	155	141	59	41	160	116	5912
			29	102	76	85	68	29	84	30	90	138	111	97	105	130	132	
			90	71	64	185	93	90	56	170	125	141	97	102	87	130	102	
			100	121	77	121	64	100	94	77	98	192	162	201	115	99	89	
Ames 1943		62	156	120	107	176	59	19	83	68	98	90	123	201	82	132	63	6480
			88	138	45	144	80	119	113	103	54	139	91	258	110	109	87	
			99	62	124	154	100	56	68	140	62	124	113	223	196	88	143	
			82	178	151	133	95	51	99	133	81	67	89	228	137	106	151	
		73	160	87	59	283	136	40	89	65	92	114	70	113	81	107	185	7077
			146	118	98	188	138	102	128	38	126	118	158	100	121	157	172	
			213	77	141	297	85	98	122	106	87	161	132	108	67	82	158	
			207	59	128	256	104	136	105	100	108	121	95	58	123	73	170	
		82	49	117	114	128	112	151	113	114	41	139	105	130	107	110	132	7159
			90	115	117	304	174	167	115	128	32	88	118	102	189	150	102	
			124	172	222	175	184	204	146	83	15	162	108	162	100	123	80	
			111	56	65	159	176	151	151	80	13	115	69	106	80	106	199	
Ames 1947		1	98	163	71	119	117	108	119	68	58	109	71	124	205	199	126	7132
			67	190	95	190	90	106	122	91	137	78	62	150	169	159	57	
			98	155	83	253	48	257	147	112	54	112	127	177	173	168	123	
			55	113	83	197	56	132	127	93	115	138	163	104	256	210	97	
		4	94	104	120	95	86	95	55	211	140	233	69	73	101	123	60	6126
			78	144	133	82	140	175	69	151	146	212	80	84	74	123	88	
			50	139	129	152	63	210	103	148	142	108	60	78	86	138	98	
			91	125	149	124	56	279	84	122	103	86	70	96	118	67	63	
		16	101	121	84	220	120	99	239	274	240	75	216	143	88	92	208	8597
			67	208	65	154	46	126	131	215	270	116	276	144	110	117	209	
			99	232	117	184	89	112	232	258	269	169	126	144	84	71	206	
			154	166	63	202	105	73	231	114	215	124	264	144	106	133	207	
		19	91	101	96	142	121	90	120	157	231	116	139	69	76	33	144	6741
			35	126	105	134	142	65	146	136	132	144	95	67	88	97	99	
			86	44	191	188	134	57	136	184	141	216	132	65	77	55	89	
			86	173	104	134	83	103	118	231	186	274	79	109	67	34	81	
		29	67	106	61	153	187	123	68	81	134	109	138	151	95	112	90	6580
			67	92	64	115	94	108	164	66	72	156	164	198	103	82	97	
			58	127	93	285	62	106	146	93	112	177	217	181	97	29	80	
			76	76	111	183	85	97	117	136	92	128	195	172	79	104	76	
		87	58	154	71	148	97	97	105	140	123	123	195	116	124	115	134	6678
			103	84	89	137	89	89	114	143	135	114	186	109	100	170	148	
			86	147	134	200	83	77	104	191	232	102	211	81	86	63	130	
			159	128	56	89	81	60	42	157	239	152	156	54	105	80	137	
F_1 Total			5352	7010	5705	8365	5366	6258	6600	6550	6644	7796	7220	6836	6600	7194	6869	100367

Table 13. F_1 hybrid egg productions of 34th generation inbred parents.

Female lines		Line no.	Male lines: Amherst 18	Amherst 22	Amherst 50	Amherst 81	Ames 1943 62	Ames 1943 82	Ames 1947 1	Ames 1947 4	Ames 1947 19	Ames 1947 29	Ames 1947 69	Ames 1947 87	F_1 Total
Amherst		18	119	57	121	81	89	121	52	227	120	111	126	55	4815
			146	116	86	42	23	239	31	104	112	138	110	163	
			57	99	41	153	113	247	277	90	144	46	102	48	
			118	84	45	82	76	215	25	120	120	147	91	126	
		22	96	144	72	36	119	94	60	64	130	226	146	139	5209
			106	39	70	91	83	94	102	40	131	216	234	103	
			96	72	98	37	141	163	132	57	163	142	161	168	
			88	93	112	254	71	157	71	141	141	102	192	70	
		50	54	142	86	124	124	141	145	156	126	68	53	110	4957
			24	209	67	158	100	146	54	149	105	116	58	135	
			57	113	128	120	159	101	81	152	80	84	128	113	
			82	179	51	94	82	102	93	210	74	89	93	174	
		81	124	75	54	85	81	154	181	131	83	94	45	144	5393
			195	75	96	82	15	232	129	91	122	100	60	211	
			118	76	74	78	121	175	242	78	39	98	99	116	
			165	105	86	92	106	220	318	142	47	249	85	142	
Ames 1943		62	105	106	111	97	96	75	138	151	74	71	143	112	4405
			134	117	40	59	56	79	78	83	114	141	82	71	
			66	124	134	24	21	84	109	120	109	161	104	192	
			147	107	81	21	73	100	34	110	119	101	87	90	
		82	105	123	165	268	108	57	285	184	149	159	151	239	8079
			235	163	187	202	124	42	257	183	176	155	183	242	
			158	323	130	244	91	75	242	135	208	147	169	251	
			146	205	191	132	90	53	254	173	197	216	169	165	
Ames 1947		1	106	123	43	176	65	216	110	88	154	195	231	121	7148
			74	141	72	188	81	200	167	96	347	213	318	153	
			287	127	58	269	33	218	136	133	276	246	240	173	
			217	62	130	122	9	228	26	54	255	269	209	122	
		4	100	113	171	133	103	173	233	109	127	107	88	148	6318
			173	142	129	81	63	180	223	125	125	249	133	119	
			87	86	158	109	58	206	229	42	177	125	133	196	
			156	118	129	152	148	228	174	117	116	101	144	175	
		19	154	194	268	231	188	198	186	128	43	182	240	216	7856
			152	190	86	182	124	183	290	87	81	224	114	237	
			159	220	183	145	79	202	178	153	5	226	193	131	
			132	185	223	268	86	144	242	70	66	236	130	207	
		29	104	204	73	146	75	220	205	152	58	79	121	129	5772
			55	228	131	267	73	176	249	75	126	99	75	64	
			125	63	141	136	109	136	230	115	87	125	78	92	
			109	214	93	130	79	152	271	191	84	91	57	74	
		69	186	62	78	120	149	295	232	122	222	191	88	92	7427
			94	185	153	163	138	275	213	107	227	211	64	133	
			158	176	117	111	117	264	221	154	225	225	44	131	
			175	154	113	86	150	222	214	174	224	209	89	109	
		87	121	141	246	128	94	40	258	54	163	108	74	120	5755
			100	92	109	127	210	151	289	53	163	81	34	138	
			75	91	134	146	150	165	171	105	152	115	124	129	
			105	108	243	150	91	195	221	25	198	109	46	72	
F_1 Total			5515	6017	5275	6085	4388	7606	7919	5227	6399	6799	5653	6251	73134

Table 14. Sources of variance for egg production on 5th, 6th, and 7th days of adult life per female for cross-combinations from inbreds after 15th, 24th, and 34th generations of full brother x sister mating.

	15th generation		24th generation		34th generation	
No. of line used		12		15		12
No. of crosses		132		210		132
Individual per cell		2		4		4
Total F_1 individuals		264		840		528
Sources of variation	D.F.	M. S.	D.F.	M. S.	D.F.	D. M.
Among R	55	2950.68	91	4762.27	55	4501.07
Error	132	1903.97	630	1176.69	396	1791.70
F		1.55*		4.05**		2.51**
Among S	54	2441.46	90	5087.67	54	7970.69
Error	187	2211.11	721	1656.98	481	2122.12
F		1.10		3.07**		3.76**
Among M	11	5831.79	14	6747.70	11	9991.30
Error	187	2211.11	721	1656.98	481	2122.12
F		2.68**		4.07**		4.71**
Among G	11	13755.56	14	14805.11	11	27077.22
Error	187	2211.11	721	1565.98	451	2122.12
F		6.22**		8.93**		12.76**

Table 15. Components of variance for egg productions of the hybrids from the three inbred generations.

Source of variation	15th generation		24th generation		34th generation		Mean
	Actual units	Percentage	Actual units	Percentage	Actual units	Percentage	
σ_e^2	1903	60.0	1176	49.8	1791	49.7	53.1
σ_r^2	523	16.5	596	38.0	677	18.8	24.4
σ_s^2	- 127	0.0	40	1.7	433	12.0	4.6
σ_m^2	240	7.6	71	3.0	228	6.3	5.6
σ_g^2	507	16.0	177	7.5	474	13.2	12.2

A common trend can be found in these tests. The uncontrolled portions of total variance, σ_e^2, furnish the largest contributions, 50 to 60 per cent of the total, in all three generations. The effects common to all progeny of the i line x the j, -- freed of the additive, specific and maternal effects, the σ_r^2 values, are next in importance, accounting for between 16 and 38 per cent of the variation. The general combining ability of the different lines contributes an average of 12.2 per cent. Maternal effects and specific combining ability are nearly equal in their contributions to the variance, -- 5.6 per cent and 4.6 per cent respectively.

Comparable calculations of combining ability have been made by Henderson on swine. With data on 8 characters, σ_g^2 has a range of 0 to 3 per cent of σ_e^2. For σ_m^2 the estimates were negative or the contributions of this factor were nil. For σ_s^2 the contributions were real, being 6 to 19 per cent of that contributed by σ_e^2. The σ_r^2 value were not significant. Our data on Drosophila egg production show distinctly higher values. Compared to the average σ_e^2 the Drosophila value of σ_g^2 is 23 per cent, σ_m^2 is 11 per cent, σ_s^2 is 9 per cent, and σ_r^2 is 46 per cent.

Sprague and Tatum (1942) have presented data on general and specific combining ability in corn. In these data the σ_e^2 term is roughly between 10 and 14. The general and

specific combining ability is calculated for 2 sets of data: one for previously tested lines in which σ_g^2 has a mean of 15.3 and σ_s^2 of 32.9 and of untested lines where $\sigma_g^2 = 43.7$ and $\sigma_s^2 = 25.5$. When these results are compared to Drosophila they show, as might be expected, that our results are more like those for the untested corn inbreds in that the σ_g^2 is larger than the σ_s^2. These corn data show values of general and specific combining which are much larger than those for Drosophila. The σ_g^2 are 1 to 4 times the error term and the σ_s^2 are 2 to 3 times the error term, σ_e^2. In our Drosophila these values are only 23 per cent and 9 per cent of σ_e^2. Obviously, general and specific combining abilities in corn play a much greater part in yield variations than they do in these Drosophila data.

Consistency of the Constants for General (g), Maternal (m), Specific (s), Sex (r) Influence on Drosophila Egg Production

In practical breeding the relative values of g, m, s, or r should be the useful guides to the breeding program if it is found by experiment that the values remain relatively constant for the same lines tested in like arrangement. The following Tables 16, 17, and 18 give the data to analyze this question.

The g values are supposed to measure additive gene action. Table 16 gives three different estimates of the g values

Table 16. Values of g and m for the 15th, 24th, and 34th inbred line crosses shown in Tables 11, 12, and 13.

	Value	g			m		
	Line No.	15	24	34	15	24	34
Amherst	18	10.4	-24.7	-15.9	4.0	13.6	-14.6
	20	....	4.6	....	....	-20.2	....
	22	1.2	-18.6	- 3.6	- 4.8	4.8	-16.8
	50	- 7.7	31.3	21.2	20.3	-11.5	- 6.6
	57	....	-24.7	....	....	9.8	....
	81	-12.3	- 8.8	- 1.7	-15.3	- 5.8	-14.4
Ames 1943	40	- 7.1	....	....	6.3	....	....
	62	4.7	- 1.9	-42.6	-24.3	- 2.0	0.4
	75	13.2	- 0.2	....	-22.3	8.8	....
	82	- 9.3	- 0.2	38.8	36.3	8.6	9.9
Ames 1947	1	....	20.4	44.0	....	-11.1	-16.1
	4	....	9.2	-19.4	....	-13.2	22.7
	16	24.9	5.1	....	-19.9	29.4	....
	19	....	- 1.6	10.6	....	2.4	30.4
	29	....	8.9	15.5	....	-10.2	-21.4
	59	-13.8	....	....	3.8	....	....
	69	....	....	- 7.3	....	....	37.0
	87	-17.9	3.2	2.9	36.9	- 3.2	-10.3
	96	13.8	....	....	-20.9	....	....

Note: F_1 means for 15th, 24th, and 34th generation inbred line crosses are 119.2, 119.5, and 138.5 respectively.

Table 17. Specific combining ability of lines shown in Tables 11, 12 and 13.

Female lines			Male lines																		
			Ashwani						Anna 1843				Anna 1847								
		Line no.	28	30	32	50	57	81	60	62	75	82	1	4	16	29	39	59	69	87	96
Ashwani		28	x	.....	38.3	-27.6	.....	-30.9	-1.1	8.1	-17.7	14.3	.....	.....	6.6	.....	.....	6.1	.....	-35.9	-1.8
				20.3	19.4	-30.4	15.7	1.3	.....	8.0	9.6	-10.4	-11.0	-4.2	-32.4	28.4	-11.7	.....	.....	-3.7	.....
				.....	-38.5	-47.1	.....	13.6	.....	21.3	.....	28.3	-17.6	21.9	.....	-1.2	-45.7	.....	3.8	-13.9	.....
		30		x	-30.5	-4.5	13.0	-7.1	.....	18.4	-29.4	-15.1	11.4	-12.9	-2.6	-9.7	1.3	.....	.....	21.5	.....
					.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		32				7.8	.....	17.8	12.5	-4.0	2.5	-19.8	.....	.....	-15.0	.....	.....	9.0	.....	-19.8	-23.4
					x	-30.0	17.0	8.2	.....	-1.2	5.8	6.6	-19.8	17.0	-17.6	4.3	14.3	.....	.....	1.4	.....
						22.4	.....	-8.0	.....	8.5	.....	-4.9	-10.2	-13.3	.....	17.0	13.1	.....	26.1	-10.2	.....
		50				.....	.....	7.9	-0.4	-11.5	19.5	-7.5	.....	.....	-1.7	.....	.....	-15.5	.....	13.3	17.7
					x	-21.3	.....	-1.9	.....	-6.0	11.1	-14.7	10.7	-2.7	17.7	1.6	11.8	.....	.....	1.9	.....
						.....	.....	-4.4	.....	12.3	.....	-12.4	-15.6	20.8	.....	3.3	-19.5	.....	-26.1	16.2	.....
		57					x	-11.0	.....	-7.9	-3.9	5.0	7.3	-16.3	-11.6	21.1	27.7	.....	.....	-7.8	.....
						.....		.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		81						x	32.1	-18.4	-19.8	17.3	.....	.....	-4.7	.....	.....	-11.0	.....	-0.7	-18.5
									.....	-13.3	-8.9	25.8	30.7	18.4	-18.9	-8.6	7.5	.....	.....	-11.2	.....
									.....	-21.7	.....	30.1	37.5	-7.0	.....	-15.8	18.1	.....	-11.6	18.2	.....
Anna 1843		60							x	-19.0	18.2	-19.0	.....	.....	-4.2	.....	.....	0.2	.....	3.5	-2.6
										.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
										.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		62								10.2	39.0		.....	.....	-4.5	.....	.....	11.2	.....	39.3	5.6
										x	-7.3	-16.1	-5.2	28.3	87.8	18.2	-4.1	.....	.....	-17.0	.....
											.....	-15.9	63.7	16.5	.....	-10.3	0.4	.....	18.1	32.5	.....
		75										19.2	.....	.....	-10.8	.....	.....	-0.1	.....	-5.6	-16.4
											x	-23.6	27.0	11.5	1.3	16.1	-26.2	.....	.....	11.3	.....
												.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		82										x	.....	.....	7.0	.....	.....	-16.8	.....	35.2	-30.9
													-29.9	-9.7	41.5	25.5	-21.9	.....	.....	30.1	.....
													19.3	8.6	.....	-25.9	-16.9	.....	22.8	1.1	.....
Anna 1847		1											x	.....	.....	.....	.....	.....	.....	.....	.....
														-4.2	-26.2	40.2	25.1	.....	.....	-24.2	.....
														-12.7	.....	41.9	95.5	.....	49.1	16.3	.....
		4												x	.....	.....	.....	.....	.....	.....	.....
															3.6	-25.6	28.8	.....	.....	8.5	.....
															.....	-33.4	51.4	.....	-9.7	-18.8	.....
		16														.....	.....	-47.5	.....	0.3	37.7
															x	-21.6	-3.6	.....	.....	8.0	.....
																.....	.....	.....	.....	.....	.....
		29															.....	.....	.....	.....	.....
																x	-45.7	.....	.....	-17.2	.....
																	-26.2	.....	23.4	23.3	.....
		39																.....	.....	.....	.....
																	x	.....	.....	-28.5	.....
																		.....	.....	46.5	.....
		59																.....	.....	18.7	60.9
																		x	.....	.....	.....
																		.....	.....	.....	.....
		69																	.....	.....	.....
																			x	.....	.....
																				-48.2	.....
		87																			-28.4
																				x	.....
																					.....
		96																			x

Note. The three figures in each cross are the values of specific combining ability for 15th, 25th and 35th generation inbred line crosses respectively.

Table 16. r effects determined from Tables 11, 12 and 13.

Female Lines		Male Lines																			
		Aderyn						Anne 1963				Anne 1967									
	Line no.	19	20	22	50	57	81	40	62	75	82	1	4	16	19	29	59	69	87	96
Aderyn	19	x																		
	20		x																	
	22			x																
	50				x															
	57					x														
	81						x													
Anne 1963	40							x												
	62								x											
	75									x										
	82										x									
Anne 1967	1											x								
	4												x							
	16													x						
	19														x					
	29															x				
	59																x			
	69																	x		
	87																		x	
	96																			x

Note. The three figures in each group are the r values for 15th, 25th and 35th generation inbred line crosses respectively.

for the line. These g values may be correlated with each other to measure the consistency of the line's performance. A high correlation could mean that the line actually has genes which are additive in their action and that environmental-gene interactions reacted the same way in each test. A low correlation might be interpreted as casting doubt on the presence in the line of such additively acting genes or that the gene environmental interactions cause pronounced changes in the additive nature of the effects. In the latter case the g values would be of little service in selecting a line for crossing to create progeny for commercial use. The correlations are shown below.

Generations correlated	Correlation coefficients
15 with 24	-0.019
15 with 34	-0.266
24 with 34	-0.168

The correlations are not significant. They are, furthermore, negative. This is disappointing. The comparison questions the additive nature of the gene action or shows the presence of significant environmental-gene interaction. In either case, the g constants would be of little help in choosing the most desirable line to continue in the breeding program. The negative correlations would come from the environment of one generation affecting certain lines favorably or unfavorably, whereas the environment of another generation was effective

on other lines in either increasing or decreasing their yields.

The m values may be tested for consistency in the same manner. The correlations are below.

Generations correlated	Correlation coefficients
15 with 24	-0.291
15 with 34	0.338
24 with 34	0.028

The correlations for the m values show less consistency than those for the g values. The conclusion appears to be essentially the same. The m values do not help us to choose lines which will behave in like manner in successive generations. Again the results point to a strong environmental-line interaction which is materially affecting the outcome of each test. This interaction predicates against the use of the m values for predictive purposes.

The s values have the following correlations.

Generations correlated	Correlation coefficients
15 with 24	0.13
15 with 34	0.02
24 with 34	0.26

These correlations are all positive but small. The s values are measures of dominance, epistasis, or like effects. The size of the correlations makes the use of the s values of doubtful value in predicting future performance of like crosses between the lines.

The r values are indicative of unequal inheritance between the sexes. The correlations for the three generations are as follows:

Generations correlated	Correlation coefficients
15 with 24	-0.16
15 with 34	-0.12
24 with 34	-0.05

The correlations are all negative and small. The negative values indicate that the parent transmitting high values in one generation reverses itself in the following generation. This fact would predicate against sex linked genes as being responsible for the observed r value or that again environmental gene interactions of some magnitude were effective agents in modifying the expected gene results. In either case, the r values have little predictive value to future generations performance.

Sprague and Tatum's (1942) data on corn may be analyzed for the stability of the estimates of general (σ_g^2) and specific (σ_s^2) combining ability in different locations, etc. Twenty-two comparisons are available. The correlation for the general combining abilities is 0.11; that for the specific combining ability is 0.08. These values are positive but low. As with Drosophila a determination of the g or s values on a line would have little predictive value for future performance.

DISCUSSION

Any individual experiment to evaluate early testing as a means of choosing superior inbred lines is beset by several unknown factors which can materially influence the interpretation of the results. These factors are not such that they can be foreseen and account be taken of them. An important factor in this group is that of chance choice of the strains which are to be inbred to form the lines. If, through chance, the strains are genetically widely divergent, then pronounced differences between strain will exist. Crosses of inbred lines between strain should give notable differences in production. If the chance choice falls on strains which are similar, despite say, widely different geographical origin, then the inbred lines formed from these strains will not differ greatly and the crosses will have only slight possibilities of showing noticeable effects.

This chance element can progress one stage further. If the strains chosen are, by chance, relatively homozygous and similar, then the inbred lines which may be derived will, in turn, be closely similar and only small yield differentials can be expected for the crosses between them. If chance, on the other hand, leads to the selection of the highly heterozygous strains, then the inbreeding process will sort out

genetically divergent lines which, in turn, will lead to crosses of markedly different yields.

The various possible combinations of these chance effects will materially influence attempts to estimate the worth of early testing as a means of selecting inbred lines having desirable combining ability. In retrospect our results indicate that the original strains chosen were not greatly different in genotype and that within the strains the possible genetically different lines were few and the differences minor. In other experiments in this laboratory much greater strain and line differences have been observed. In a sense the choice of the material for this study was not particularly lucky. The study evaluates early testing under its most difficult conditions.

To the questions proposed for study, the data collected return largely negative answers. Early testing of the lines by means of crossing the inbred lines to our synthetic strain gave little or no information on the lines worth in subsequent crosses. The performance of the inbred lines themselves did give some indication of their relative yield in later generations but the correlations were small, about 0.25. Egg yields for inbred x synthetic crosses were actually larger early in the generations of inbreeding than for like crosses of later generation inbred x synthetics. The general and specific combining ability in these strains was, on the whole, small,

at least as compared with corn lines. The ratio between general and specific combining ability did take the same direction as those for corn. Lines derived from previously untested material showed more general than specific combining ability.

One condition of some importance to these experiments was overlooked in the original planning. The tests of the different inbred generations are confounded to some degree with any seasonal effects which could penetrate the rather severe controls thrown around the experiments. Unknown types of seasonal effects may have influenced the egg yields of the different generations tested in a progressive manner. Such changes might, in part, account for the progressive shifting of the hybrids average egg yields with generation of inbreeding. It would have been desirable to have had controlled random bred stocks for each strain tested with each set of crosses to furnish information on these unknown factors.

The inbred strains, despite the continued natural selection toward genetically better producing lines due to the elimination of those without progeny, continued to decline in egg yield at nearly a uniform rate throughout the experiment. In so far as this was due to changes in gene frequency within the lines, the process appears to be one capable of indefinite continuance. The reservoir of genetic variability does not decline rapidly.

A characteristic of these data is a maternal effect on

the egg yields of the reciprocal crosses. The progenies of synthetic females were poorer layers than the progenies of synthetic males. As the genotypes of these reciprocally formed females should be the same, the effect must be maternal. It appears as if the synthetic females laid a smaller egg or some like factor. This maternal effect could be genetic but if so, must be a carry over of the female's genotype.

General and specific combining ability in these Drosophila data control roughly 12 and 6 per cent of the variation in egg yield. Compared to corn as analyzed by Sprague and Tatum (1942) the influence of these factors on yield is very low, only 1/4 to 1/3 those observed in corn. With swine, on the other hand, this comparison is favorable to Drosophila where general combining ability is 6 to 8 times that for swine, Henderson (1948).

Values of general and specific combining ability do not seem to be of too great importance in either corn or Drosophila as they are not consistent from test to test. The correlations for general combining ability were low, ranging from 0.11 to -0.27. For specific combining ability the range was 0.02 to 0.26. More accurate methods of evaluating inbred lines for their performance in cross are to be sought.

It is of more than passing interest that, despite the almost random rearrangement of the line crosses in successive tests, the yields of the F_1 are 25 to 50 per cent greater

than the inbred lines from which they were derived. There is in these results a suggestion of the effects of unlike alleles in the same loci creating better conditions than when like alleles fill the loci.

SUMMARY

Progeny from three strains of Drosophila melanogaster were used as foundation stock to establish the inbred lines utilized in these experiments. Matings were throughout full brother x sister in single pairs. A synthetic stock derived from 8 inbred lines was used as the tester parent in the crosses. A 3-day laying period, 5th, 6th, and 7th day after emergence, was standard throughout these experiments.

Three sets of data were collected: (1) the hybrid egg laying performance from different generation inbreds test-crossed to the synthetic stock; (2) egg yields from pure line flies after more than 20 generations, and (3) egg yields of single cross progeny resulting from mating individual inbred lines in all possible combinations.

Real differences in the combining ability between strains were found in first generation inbreds crossed to synthetic testers. Ames 1947 had the highest average egg record 178.8 ± 2.5 per fly. Ames 1943 was second with 176.2 ± 2.7. Amherst was last with 166.2 ± 2.8 as the average for its flies. The average standard deviation is around 60 eggs. The average coefficient of variation is about 35 per cent. The distributions for the egg productions of the 3 strains' hybrids are continuous and symmetrical.

Inbreeding does not stabilize the egg productions of the different synthetic x inbred crosses. Instead, the egg productions of these test hybrids decrease steadily at the rate of about 2.4 eggs per generation.

The degree of heterosis exhibited by inbred lines crosses increases with the generation of inbreeding from the 15th, 24th and 34th generations. The average percentage increases of the hybrids over the parents are 17.2%, 30.2%, and 62.4% in the 15th, 24th and 34th generation respectively. The inbreds showed lowered vigor and productiveness as inbreeding advanced but this loss of vigor is not detrimental to the egg productions of the hybrids made from these inbreds.

Inbred lines with more than 20 generations of brother x sister matings show downward general trend in productivity. The average strain egg production is reduced 4.3 eggs or 3-4% per generation of inbreeding.

Uncontrolled variations contribute most of the variations in egg production. Differences between reciprocals appear due to the synthetic females being poor mothers. Line differences are small and irregular. Strain differences are large in the first generation. Continued inbreeding has caused an increasing separation of the strains' egg productions.

Within inbred lines, after 20 generations of brother x sister matings, the uncontrolled variances are similar in the successive generation tests. The pure inbreds have 68% more

line within strain variance than was observed for the inbreds x synthetic over the period covered by the same generations. The strain differences are not significant.

No trend was found in the correlation coefficient between successive tests on the same top crosses. The top cross tests, thus, contributed no information of value for predicting subsequent performance in later generations.

General combining ability, maternal influences, specific combining ability and the effects of reciprocal crosses freed of additive, specific and maternal effects show small effects on line cross performance. The uncontrolled portion of the total variance, σ_e^2, contributes most to the variance, 60%. Taking σ_e^2 as a standard for comparison σ_g^2 is 23%, σ_m^2 is 11%, σ_s^2 is 9% and σ_r^2 is 46%.

Correlation coefficients between general combining ability, g, values of three different generations are negative and small.

Correlations for the maternal effects are small and inconsistent. Values for specific combining ability are positive and small. Those for r are negative and small.

The lack of stable estimates for the performance of the different inbred lines suggest strong environmental-genotypic interactions of direct significance to successive yields of the same line crosses.

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